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## CONTENTS

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No. 4 (*Published September 19, 1957*)

No. 5 (*Published October 29, 1957*)



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# On the Variation in Bottom Fauna and Fish Yield in Relation to Trophic Level and Lake Dimensions[1]

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ABSTRACT

The relation of area to depth was studied for 500 lakes. Up to 0.3 km.$^2$ the mean depth is constant at 3 to 4 m. This is probably an artifact due to omission of shallow lakes from study. From 0.3 to 300 km.$^2$ the relation of depth to area is linear on a log–log plot. In the largest lakes the depths increase less proportionally.

Of the three ways to study fish productivity in lakes, one, the estimate of standing crops, is usually attempted at mean depths around 1 m. Another, angling returns, centers on lakes of 3.5 m., while commercial reports come from lakes of 6.5 m. average depth, and extend to the deepest lakes.

Fish records can be conveniently divided into three trophic levels, short food chain, e.g. carp, intermediate, e.g. bluegills and long, e.g. trout, bass. Records are interconvertible by use of factors. By factoring, a productivity index is calculated for some 150 lakes.

The productivity index is found to be inversely proportional to mean depth on a log–log plot. Thus by correction of the PI it is possible to derive a theoretical value, called the quality index, for a standard lake 5 m. deep.

The QI is intended to screen the effect of depth out of the PI and so disclose the inherent capacity of the lake. The QI values vary around unity. Lakes of mean depth under 2.5 m. are factored as of that depth, it being assumed that primary productivity due to photosynthesis goes on all the way to the bottom.

A study of bottom fauna in 250 lakes in several regions gave no indication of a relation between depth and productivity.

## I. INTRODUCTION

One of the central problems of theoretical limnology is the assessment of the productivity of lakes. One of the central problems of practical limnology is the manipulation of lakes with the view of increasing their productivity. Both these aims are somewhat put off by the lack of common standards of measurement with which to compare lakes of different regions, and to compare information of different kinds. In recent times efforts have been made to assess productivity by chemical studies on the water or sediment. The results frequently suffer from the disadvantage that they cannot be compared very readily with direct observations of the life within the lake. We have in effect a sort of quantitative measurement on the Y axis of a plot without a comparable series of measurements on the X axis which might serve as a standard. For example, Pearsall (1930) used the percentage of arable land in the drainage basin of each lake as a standard of quality, that is to say the amount of land on which farmers believed they could earn a living. This is certainly a promising approach, although what is

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called arable land in one region might not be so designated elsewhere. Moreover most of the lakes in which angling is carried out do not have arable land in their drainage basins. Direct chemical study of the soil would ultimately be necessary. Some interconversion with the crop in the lake itself would also be needed before such a system could be placed on a firm basis.

In any attempt to arrive at a number describing the inherent productive capacity of a lake, it will first be necessary to screen out local peculiarities. With fish, for example, the information is of three kinds, standing crop, angling catch, and commercial catch.

The techniques for obtaining records about the types of crop, differ in a way that is reflected in the depths of lakes selected for study. Thus, as Figure 1 shows, standing crops are estimated for the most part on lakes of depth about 1 m. Angling catch is studied in somewhat deeper lakes, centering on 3.5 m. (and having also greater area). Commercial fisheries do not exist on very small bodies of water but are reported from large shallow lakes as well as large

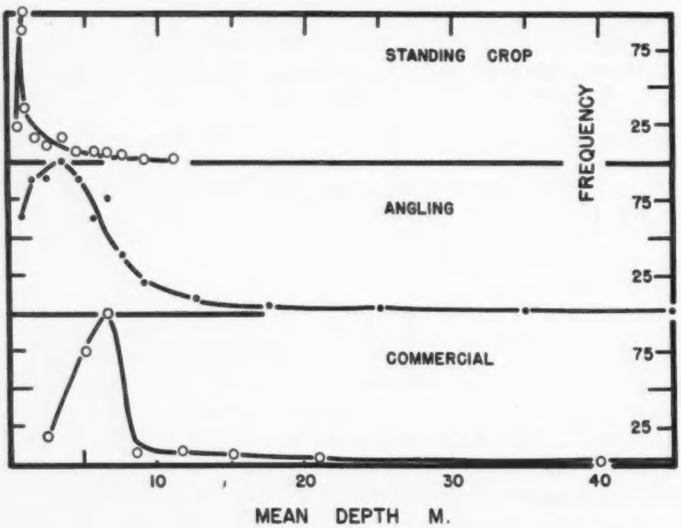


FIGURE 1.—Depths of lakes selected for fish estimates of three kinds. Maximum frequency of selection is called 100 in each. Evidently studies of standing crops have not been made on deep lakes, and there is a preference for selection of waters shallower than 1 m. The steepness of the standing crop peak is considerably dependent on Bennett (1943) who studied 22 ponds in Illinois, of which all but four were less than 1 m. in depth. Without his group the fall to the right would be more gentle. For angling returns, the peak frequency centers on 3.5 m. and half of all lakes studied lie in the mean depth range of 2 to 6 m. The commercial peak centers on 6.5 m. and tails off to the right beyond the chart, all the way to Lake Superior (149 m.).

deep lakes. The peak frequency occurs at 6.5 m. which is perhaps shallower than might have been anticipated. The study extends to lakes of greater depth than by other methods, eventually to Lake Superior.

It is a matter of general knowledge that the mass of fish which can be supported depends on the trophic level, or food-chain length, of each species. Thus the crop of carp will be a good deal higher on the average than that of trout. Then there is what might be called the effect of aquatic climate. Within the temperate zone, the general climate, as determined by latitude, would seem to be negligible in comparison with the local conditions around the lake. There are often within a short distance of each other, lakes which maintain cold water during the summer and others which are warmed throughout. Such differences will evidently affect the standing crop. Finally the dimensions of the lake will have to be taken into consideration as there is evidence that large lakes and deep lakes are not on the average as productive as small shallow ponds.

It appears to be generally thought that the capacity of a lake to supply nutrients, for the support of life, is an area phenomenon dependent on regeneration from the sediment, and on rainfall on the water or drainage basin. On the other hand the availability to organisms must be a volume phenomenon, inversely proportional to the amount of water in the lake, hence to the mean depth. This is what might be called a dilution factor, which determines how much nutrient the plant, or eventually fish, can get at in its vicinity. Reference to an aquarium will clarify the point. Here the amount of growth depends on the quantity of nutrients added to the water. There being no exchange reservoir of soil to renew the nutrients as used, the concentration in the water has to be kept high, about two orders of magnitude higher than in a lake. The principle, however, is the same.

The dilution effect will scarcely be felt when the lake is so shallow that its whole depth is occupied by plant life, for here the plants can reach all parts of the water. Its beginnings might be expected at depths of a few meters, where some of the water fails to support plants owing to absence of light. Thus allowance for dilution should not be applied to very shallow ponds. It is not applied in this paper at less than 2.5 m. mean depth.

The deeper the lake the clearer and more decisive should be the dilution effect, i.e. the dependence of productivity on mean depth. So long as the lake is stirred twice a year it would not seem to matter whether it is stratified or not. Once material from the depths has been mixed through the lake it will enter into secondary equilibria with the solids, plants, etc., in the shallow zone and be available as needed.

The above considerations deal with organisms in the water. What about bottom forms? Here the problem differs, for these organisms are surrounded by settled sediment, such as it is, from the drainage basin. They could hardly be dependent on the rate of its return to the free water. Thus we might expect that the quality of the sediment and not the volume of water would determine the mass of bottom organisms. Conversely, the bottom fauna might be a direct index of quality of the watershed.

If it should happen that a series of lakes were chosen, among which the shallow ones (as is likely) were in flat country, perhaps prairie or agricultural land, while the deep ones (as is likely) were in rugged, inhospitable surroundings, then an apparent relation of bottom fauna to depth might be observed. This would perhaps be an artifact which would not be representative of world lakes.

The bulk of the present paper is taken up with an attempt to make allowance for the factors mentioned in so far as they concern fish. It is evidently desirable also to compare fish production with that of higher plants, plankton and bottom fauna. The last mentioned of these receives some consideration below.

## II. FISH

### Allowance for Type of Information and Trophic Level

It will be obvious that if we are to find a common basis for the comparison of lakes, we shall have to factor separately for standing crop, angling and commercial catch. The selected method is to find numbers by which the average masses of fish in North American lakes may be divided in order to give a value of unity. Where necessary, allowance is made for apparent trophic level, and sampling bias. Consider first, item four of Table I which deals with annual commercial catch. In this instance no allowance for trophic level was needed. The number 5.2 by which the catch is divided in order to give a value, or productivity index, of unity, is the average of recorded commercial catches from 22 lakes under consideration. These include 18 natural lakes, mostly fairly large, and among which are the Great Lakes. The catch here consisted of whitefish, trout, pickerel, etc., and averaged 4.5 kg. per ha. There were also three reservoirs in Tennessee, as well as Clear Lake, California, making up the group.

Table I.—Factors by which individual lake records are divided in order to bring them to a comparative basis called the productivity index. The factors represent the mean supporting capacity of lakes, in kg. per ha. Standing crop values are based on Carlander's (1955) tables 6–8. Angling and commercial catches come mainly from records on lakes listed in this paper.

| Fish | Standing crop | Annual angling catch | Annual commercial catch |
|---|---|---|---|
| 1. Gizzard shad; buffalo; carp | 140 | | |
| 2. Bluegill, etc. (*Lepomis*); crappie; bullhead, catfish | 43 | 20 | |
| 3. Bass (*Micropterus*, *Morone*, *Ambloplites*, *Chaenobryttus*, *Lepibema*); yellow perch; bowfin; gar; pike, etc. (*Esox*); also *Stizostedion*; trout; whitefish | 16 | 4.7 | |
| 4. All species | ... | ... | 5.2 |

For these last the average catch was 8.6 kg. per ha. and consisted of such things as catfish, bullhead, and a few carp and drum. Putting these results together we obtain for all a value of 5.2 kg. per ha. which has been entered in Table I, as the factor by which any commercial catch should be divided in order to produce the productivity index for that lake. It will be evident that a larger series would have necessitated some division between the catfish–bullhead group and the whitefish–trout group of lakes. However, the evidence is too scanty to attempt any trophic distinction, and no serious error will be introduced by treating them together at this stage. When the value of 5.2 was first established it was thought that it would be necessary to adjust it for depth, since the commercial catch takes in the deepest lakes. However, it turned out that 5.2 was usable without further manipulation.

Treatment of the remaining groups in Table I was suggested by a recent paper of Carlander (1955). His analysis showed that species with relatively short food chains, such as the gizzard shad, buffalo, carp and sucker, have rather high standing crops; small insectivorous fishes such as bluegill, other sunfish and crappie, have intermediate standing crops; and the higher predators, such as the largemouth bass, walleye, and pike have relatively low standing crops. Trout may variously belong in the insectivorous or predator group. At each level there are secondary species which have low standing crops and never seem to attain predominance, for example the carpsucker, warmouth and rock bass. Species at the same food level are not necessarily in competition, the presence of two or more species in a lake for many years being evidence that competition between them is not complete.

Carlander found it convenient to consider standing crops in three groups, fish with short, intermediate and long food chains. The groups populated lakes at different mass levels and did not interfere with one another. Within each group there was no systematic tendency for increase or decrease of any given species in relation to the number of other species present. Thus it appears reasonable to total the species at a given trophic level and call the mass obtained the supporting capacity of the lake as measured at that level. This has been one of the principles followed in setting out the numbers in Table I.

A second necessity in constructing Table I was to make allowance for the fact that certain species which turn up in standing crop estimates, are not taken by anglers or commercial fishermen. These include such fish as the sucker and golden shiner. Evidently we shall not be able to compare angling returns with standing crops if we include, in the latter group, species which are rejected in the former. Thus in addition to making allowance for trophic level, certain species were omitted from the calculations of standing crop estimates. Table II shows some examples of species omitted.

The standing crop estimates in Table I are based on the extensive information compiled by Carlander (1955). For fish with short food chains (Group 1) the value given represents the average of records for gizzard shad, buffalo and carp. For Group 2, consisting of bluegills, etc., the records shown in Carlander for fish with intermediate food chains have been averaged to yield the value

TABLE II.—Examples of the method of treatment of fish weights to obtain an index of productivity. Group O includes casual species, not reported in angling or commercial catches, hence not included for computation of standing crop indices. Group 1 is also scarcely existent among sport or commercial records, but occurs frequently enough in standing crops to yield a reasonable factor. Groups 2 and 3 are used either for standing crops or angling. The Group 4 factor is applied regardless of species to commercial catches. Within each group the species counted are summed up before being divided by the factor. Where two or three indices are available (e.g. Homewood Lake) the highest is chosen, so that the lake is counted at the trophic level where it is expressing itself most productively.

| | Michigan comml. | Boar's Back, N.S. St. crop | Opeongo, Ont. angling | Homewood, Ill. St. crop | East fish, Mich. St. crop | Claytor, Va. angling |
|---|---|---|---|---|---|---|
| | *Except for productivity index values, data represent kg. per ha.* | | | | | |
| 0. *Not counted* | | | | | | |
| Eel | | 0.20 | | | | |
| Golden shiner | | 0.40 | | 10.10 | | |
| Killifish | | 0.20 | | | | |
| Minnow | | | | | 2.50 | |
| Sucker | | 9.10 | | | | |
| 1. *St. crop factor* 140 | | | | | | |
| Buffalo | | | | 139.20 | | |
| Carp | | | | 157.20 | 9.00 | |
| Gizzard shad | | | | 215.90 | | |
| Productivity index | | | | 3.66 | 0.06 | |
| 2. *St. crop factor* 43, *Angling factor* 20 | | | | | | |
| Bluegill, sunfish | | | | 140.80 | | 0.17 |
| Bullhead, catfish | | 4.60 | | 19.20 | | 0.17 |
| Crappie | | | | 61.40 | | 0.69 |
| Productivity index | | 0.11 | | 5.15 | | 0.05 |
| 3. *St. crop factor* 16, *Angling factor* 4.7 | | | | | | |
| Bass | | | | 39.20 | | |
| Trout | | 0.10 | 0.30 | | 1.20 | 0.87 |
| Yellow perch | | 4.40 | | | 20.90 | |
| Productivity index | | 0.28 | 0.06 | 2.45 | 1.38 | 0.19 |
| 4. *Comm. catch factor* 5.2 | | | | | | |
| Whitefish, trout, etc. | 1.80 | | | | | |
| Productivity index | 0.35 | | | | | |
| Chosen productivity index | 0.35 | 0.28 | 0.06 | 5.15 | 1.38 | 0.19 |

of 43 kg. per ha. For Group 3, including bass, etc., the Carlander figures for bass through catfish have been averaged and yield the value of 16.48 kg. per ha. On a first trial a group including pike, trout, whitefish, etc. were averaged to yield an additional standing crop level. However, for the best studied member of this group, the trout, the result was an absurdity which is discussed below. After some consideration it was decided to include the trout with the basses, yellow perch, etc. This procedure appears to have produced reasonable results.

For computation of the angling yield the mean values of the three classes under consideration were averaged for the lakes listed in Table VIII. Group 1,

including carp, etc., had angling reports from only three lakes with an average of 0.23 kg. per ha., a ridiculous figure. Either anglers do not wish to take carp or biologists do not wish to record successful carp fishing. No use has been made of the three carp records, and no carp factor is included in Table I. For Group 2 the average of 23 records was 20 kg. per ha. which is included in the table. It may be taken that at equilibrium the ratio of standing crop to angling catch gives a rough indication of the time necessary to produce a catchable fish, i.e. the breeding speed. For Group 2 the ratio is $43/20 = 2$, a figure which appears reasonable, as suggesting that the standing crop can be reproduced every two years. Turning to Group 3 (bass, etc.), the average was 4.7 kg. per ha., not taking trout into consideration. This also appears to be a reasonable figure, suggesting that fish of this group require on the average something like three years to recoup their angling losses ($16.48/4.7 = 3.5$). Trout were considered separately, as discussed below; and after rejecting the average findings they were included, together with pike, etc., under Group 3, as had been done for the standing crop values.

The procedure then, is to take the recorded crop of each lake, sum up the weights of the different species into the appropriate groups outlined in Table I, divide each group by the appropriate factor and call the result a productivity index by which to compare that lake with others. As already mentioned, certain species are rejected when considering standing crops. There may be one, two or three separate productivity indices obtained from standing crops, one or two indices from angling catches and a single index from the commercial catch. Examples of the application of the method are shown in Table II. Where more than one index is obtained the higher one is accepted. This seems reasonable because warm-water lakes will naturally support warm-water fish, often of Group 2, to the exclusion of trout, etc. On the other hand cold trout waters will express their productivity as trout rather than as bluegills, etc. In other words the highest index reflects the productivity type most "congenial" to the lake in question.

In Table III are compared all the lakes in which two sources are available for calculation of an index. There are no lakes, in the list with three kinds of record. The sets of duplicates in Table III do not show any systematic differences; on the average the alternate readings are within 3% of each other. Some comments on the lakes follow.

Southport Pond, Prince Edward Island, is exclusively trout water. Its standing crop was determined by drainage after the fishing season. The angling catch is typical of several Prince Edward Island Ponds observed over some years. Agreement between the two values is close.

Copper Lake, Nova Scotia, had its standing crop estimated by a single capture-mark-recapture experiment on trout, together with poisoning of the shallows over five years. The estimate is presumed minimal. The angling index rose from 0.21 before poisoning to 0.43 afterwards, the latter value approximating the standing crop index.

TABLE III.—Lakes where information permits establishment of a productivity index on two of the three bases of estimate. There is no evident systematic difference between the sets of values. If one expresses each right hand estimate as a percentage of the left, the average for all is 97%.

| | Index | | | |
|---|---|---|---|---|
| | Standing crop | Angling catch | Comml. catch | Reference |
| Southport Pond, P.E.I. | 6.88 | 8.72 | | Smith, 1955, priv. comm. |
| Copper Lake, N.S. | 0.36 | 0.21<br>0.43 | | Hayes & Livingstone, 1955 |
| Pyramid Lake, Alta. | 0.61 | 0.19 | | Rawson & Elsey, 1950 |
| Lac La Ronge, Sask. | | 0.19 | 0.21 | Rawson & Atton, 1953 |
| Sugarloaf Lake, Mich. | 1.38 | 1.57 | | Cooper, 1952, Hazzard & Eschmeyer, 1938 |
| Fife Lake, Mich. | 1.29 | 2.19 | | Eschmeyer, 1936, 1937, 1939. Cooper, 1952 |
| Clear Lake, Calif. | ... | 0.70 | 0.54 | Murphy, 1951 |
| Shoe Lake, Ind. | 3.30 | 2.24 | | Ricker, 1942a |

With Pyramid Lake, Alberta, we come to a discrepancy, explicable by sport fishing preference. The most abundant fish (outside of suckers) was the mountain whitefish, not highly regarded as a game fish, hence overlooked by anglers. The fish mainly sought (80% of catch by weight) was the lake trout, which made up only 1.7 of the total 9.8 kg. per ha. in the game fish standing crop. It thus appears that when anglers will not take major components of the fish population, the angling index will be low.

Lac La Ronge, Saskatchewan, whose fishing is made up mainly of whitefish, lake trout and pike, shows similar angling and commercial indices, both low. It is a northerly lake in the barren Canadian shield region, so that the low index does not occasion surprise.

In Sugarloaf Lake, Michigan, the standing crop and angling indices for bluegills, etc., are respectively 0.61 and 0.60. For bass, etc. they are 1.38 and 1.57 as shown in the table. Duplication is close despite the fact that measurements were published many years apart and by different workers.

Fife Lake, Michigan, somewhat similar to the above as to crops and observers, shows a greater discrepancy between indices.

Clear Lake, California, has its angling made up largely of catfish and its commercial catch of blackfish (*Orthodon*). There were also 4.8 kg. per ha. of carp taken commercially which, as already noted, are omitted when computing the index.

Shoe Lake, Indiana, gave Group 2 indices for standing crop and angling of 3.30 and 2.24. For Group 3 the values were respectively 1.51 and 1.43. Ricker gives fiducial limits on all estimates, from which it is evident that 3.30 and 2.24 are not significantly different.

Comparing Sugarloaf and Shoe Lakes, it is evident that the former yields its maximum index with bass, etc. (Group 3) and the latter with bluegill, etc. (Group 2). Thus the productivity index might be used to show the trophic level at which the potentialities of a lake are best expressed. In the present paper this aspect is not developed, the object being to compare lakes at their best

index, in whichever group it occurs. As a matter of practice all three groups are in use for consideration of standing crops, whereas Group 1 (carp, etc.) is of no help with angling data. Commercial records are very largely from Group 3 (usually whitefish and lake trout) and there is no suggestion from the records that accuracy would be improved by use of more than one factor.

Mention may be made of two Wisconsin lakes, Kegonsa and Waubesa (Frey and Vike, 1941; Helm; Hacker). The lakes are not included in Table III although duplicate estimates of a kind exist. They were overrun with carp and seined systematically for a period of years in an effort (unsuccessful) to reduce the population. If the seinings are taken as a minimal value for a standing crop of carp, they yield indices of 1.47 and 2.36 respectively. By contrast the angling indices are 0.46 and 0.63.

It might be presumed that carp is depressing the supporting capacity of the lake for game fish. There is no other direct evidence in our lists bearing on this point, although the view is widely held and receives some support from data on midwest reservoirs (Carlander, 1955, tables 13, 14).

### The Anomalous Position of Trout and Carp

Sampling bias may enter many poisoning, draining or netting experiments because the purpose is to rehabilitate fertile waters which are overrun with short-food-chain fish, in the hope of encouraging more desirable species. This would make standing crop values for carp, etc., tend to be high. On the other hand, he would be a bold biologist who undertook to poison a better than average trout-producing lake for census purposes.

When it comes to angling data the tendency is to select high-producing trout lakes for study. Carlander (1950, 1953) provides tables of annual trout yield. If we take each mass range, and weight it for the number of regions represented, an average is obtained for the whole (including some European values) of $21.7 \pm 6.9$ kg. per ha. Angling data as used in this paper, similarly weighted, give $17.0 \pm 5.1$ kg. per ha. annually. As against these, Carlander (1955) sums up the continental average for standing crop of trout as 4.6 kg. per ha. (excluding only managed lakes in Wisconsin). To maintain the reported fishing level, in the presence of the reported standing crop, the trout mass would have to be replaced about four times annually. In fact it takes two or three years for replacement. Thus the two measurements, standing crop and angling success, distribute between them an error of a whole order of magnitude. Trout being fish of great interest, it may be supposed that bias about their abundance is maximal.

Suppose the discrepancy between the measurements just discussed to be equally attributable to angling and standing crop records. Then the former should be reduced by $17.0/3.3 = 5.1$ kg. per ha., while the standing crop should be given as $4.6 \times 3.3 = 15.2$ kg. per ha. These values are very close to the factors actually used for trout, together with other Group 3 fishes in Table I.

With carp also, angling preference, makes the returns differ from random sampling. Possibly the average standing crop of 140 kg. per ha. is influenced by

the effort to rid waters of these undesirable fish. On the other hand the sport catch of 0.2 kg. per ha. (based on only three lakes) reflects the distaste of anglers. Two lakes in Wisconsin studied over many years, showed angling averages of 0.02 and 0.07 kg. per ha. At the same time a seining programme intended to reduce the population, yielded averages of 330 and 206 kg. per ha. of carp without attaining the desired reduction (Frey and Vike, 1941; Helm). The commercial catch of carp in four places (three reservoirs in Tennessee and one California lake) was uniformly low, the mean being only 3 kg. per ha., evidently quite different from the Wisconsin seinings (Bryan and Tarswell, 1941; Murphy, 1951). Thus there appears to be no real indication of productivity obtainable from angling and commercial returns on carp.

### Effect of Climate

This subject will be dealt with very briefly. All the lakes here considered are in the temperate zone and subject to seasonal fluctuations. Any differences due to latitude are in all probability overwhelmed by local differences from lake to lake. Thus a shallow Illinois pond would be expected to support fishes of Groups 1 and 2 and perhaps occasionally Group 3, with the omission of pike, trout, etc. If such a pond were uniformly warm it would express its productivity perhaps in the form of bluegills or crappies. On the other hand a mountain lake would be unlikely to express itself in the form of warm-water fish, but might have a high yield of trout, if it had a high native productivity. It would seem, therefore, that the method of expressing productivity, through the factors in Table I, automatically cares for climatic differences from lake to lake, yielding a value finally which reflects the inherent capacity of the lake soil to support fish life.

It seems quite possible that the Table I factors could be applied to shallow tropical ponds in order to compare the productivity of these with temperate lakes. On the other hand it is doubtful whether a deep tropical lake, with warm water throughout, and without any regular turnover, could be brought into the scheme. Such lakes are so warm that mineralization of organic matter occurs while it is sinking to the bottom (Ruttner, 1953).

### Effect of Lake Dimensions

In 1946 G. A. Rounsefell published an interesting paper suggesting that the production of fish in lakes varied inversely with area. Thus when a log–log plot of pounds per acre against area was made, a significant relationship held. Either total population, sport yield or commercial yield could be used. Of other factors which might contribute to productivity, Rounsefell remarks that "the relative area of fertile shallow water is generally much less in proportion to total area in the larger lakes than in the smaller ones" and "even in lakes which are comparable physically and chemically the yield may differ considerably because of a difference in the species present".

More recently Rawson (1952, 1955) has dealt with the effect of the depth of very large lakes on commercial fish production, as well as bottom fauna and

standing crop of plankton. With all three he finds that the greater the depth the lower the productivity.

It seemed worthwhile, as a preliminary, to enquire whether large lakes tend to be deeper than small ones. A graph summing up information on this point is given in Figure 2. This is based on some 500 lakes scattered over the world, sources of information being given in the bibliography. A log–log plot has been used since it has well-known advantages in the calculation of errors. The lengths of the vertical and of certain horizontal lines represent standard errors. The lakes have been treated in groups of sixteen, except for the very largest ones where not so many were available.

For most of the lakes studied the mean depth was stated or was obtainable from contour maps. The ratio of maximum to mean depth was calculated for all lakes in which the authors gave full information. The ratios, taking lakes in groups of 20, are given in Table IV. The theoretical ratio, considering the lake as a cone would be 3, but this is not reached in any group. For most lakes up to areas of say 10 km.$^2$ (at any rate up to something above 3 km.$^2$) the ratio shows no trend, averaging 2.35. For larger lakes there appears to be an approach to the theoretical value.

TABLE IV.—Data on lakes to see whether a trend exists with increasing area in the ratio of maximum to mean depth. The lakes selected are those on which the authors gave full information. The mean ratio for the first seven groups is 2.35. For larger lakes there is an approach to the theoretical ratio of 3.

| Number of lakes in sample | Mean area *km.*$^2$ | Ratio max. to mean depth |
|---|---|---|
| 20 | 0.02 | 2.36 |
| 20 | 0.09 | 2.43 |
| 20 | 0.20 | 2.25 |
| 20 | 0.40 | 2.36 |
| 20 | 0.73 | 2.19 |
| 20 | 1.43 | 2.43 |
| 20 | 3.10 | 2.44 |
| 20 | 13.00 | 2.89 |
| 20 | 91.91 | 2.72 |
| 7 | 466.00 | 2.97 |

In those lakes for which an author provides maximum but not mean depth values, or where soundings are inadequate, the factor of 2.35 has been used for conversion.

Figure 2 shows that from an area of some 0.3 km.$^2$ to some 300 km.$^2$ the relation of depth to area is linear on this plot. In the very largest lakes the depths do not increase as much proportionally. The lines have been calculated from the points by the method of least squares. An interesting phenomenon occurs in the smallest bodies of water. Evidently average limnologists do not report on waters of mean depth less than 3 or 4 m. Presumably such shallows are often unstable, tending to dry up in summer to some extent, and perhaps lacking interest to people concerned with lakes. It is likely that the direct relationship

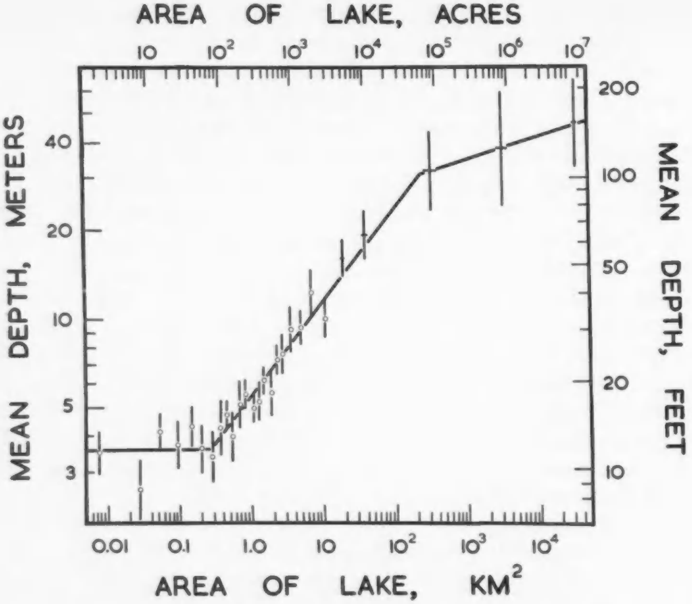


FIGURE 2.–Logarithmic plot showing relation between lake area and lake depth, based on some 500 lakes in various parts of the world. For sources see bibliography. Each point is the average of 16 lakes (except for the two largest where only nine per point were available). Vertical lines indicate standard errors of depth. For the five final points dealing with large lakes the standard errors of area are also shown by the lengths of the horizontal lines. The three parts of the curve (which are calculated lines) show that for lakes of less than some 0.3 km.$^2$ (50 to 100 acres) there is no recorded increase of depth with area, the average depth being 3.6 m. From 0.3 to 300 km.$^2$ there is a regular increase of depth with area. In the largest lakes (three final points) the slope is diminished.

between area and depth holds also below 0.3 km.$^2$ but this fact is not evident from the literature.

The straight-line relationship of the central part of Figure 2 makes it probable that Rounsefell's list of records could be as well related to depth as area. By examination of the original papers and correspondence with authors, the mean depths of all but two of the ponds or lakes mentioned by Rounsefell have been secured and, for comparison to his Figure 1, the regression has been calculated of log fish weight on log depth. The graph is not published here, but Table V compares the standard errors of Rounsefell's lines and those obtained in the corresponding depth plot.

The differences are small, the depth treatment being slightly better as regards total population and sport fishing, and slightly poorer as regards commercial fishing. However, in a depth plot the annual commercial catch has a less steep

TABLE V.—Comparison of the standard errors of Rounsefell's (1946, Fig. 1) plot of lake area *vs.* fish weight, with a plot of mean depth *vs.* fish on the same lakes (less two for which depth was not obtainable). The differences are not great, two being lower in the depth regression and one in Rounsefell's treatment.

| | Rounsefell: based on area | This paper: based on depth |
|---|---|---|
| Total population | 0.50 | 0.45 |
| Sport fishing | 0.48 | 0.46 |
| Commercial fishing | 0.29 | 0.32 |

slope and is relatively lower than in Rounsefell's area treatment. Actually according to Rounsefell the annual commercial yield would extrapolate into small bodies of water at a level above the total population. With a depth plot it occupies a more reasonable position. In summary then it appears that Rounsefell's productivity data could have been at least equally well presented on a basis of depth rather than area.

If the true relationship of productivity is with depth, area being incidental, it would follow from Figure 2 that an area plot would be unsuitable for lakes of less than 0.3 km$^2$, i.e., for about half the lakes to be considered below.

EFFECT OF THE ILLINOIS PONDS

The anchor holding in place the top left-hand corner of any complete regression of fish crop on area or depth, consists of 22 Illinois ponds described by Bennett (1943). These ponds are small, shallow and fertile. Many of them contain quantities of short-food-chain fishes.

Bennett (1955, private communication) gives some information about the group. Illinois, he says, may be divided into three sections from the standpoint of fertility and crops: a northern and central black prairie region where corn production without fertilizer is 75 bushels per acre; a south-central section of grey prairie where corn production on unfertilized land is 25 bushels per acre; and a southern Ozark section where the land grows nothing but broom sedge and sassafras trees unless fertilized.

All the Illinois ponds used by Rounsefell, with but two exceptions, were in the black prairie region of Illinois. Waltonian Pond, the only one in the Ozark region, supported 71 pounds of fish per acre. The average for the remaining 21 ponds was 464 pounds per acre.

TABLE VI.—Values for four logarithmic plots of area or mean depth versus productivity index. The $r$ values show that all four are highly significant. Areas are in km.$^2$ and depths in metres. For list of lakes see Table VIII.

| | Number of lakes $n$ | Intercept $a$ | Slope $b$ | Correlation coefficient $r$ | Standard error of line $\pm\sigma$ |
|---|---|---|---|---|---|
| All lakes, depth plot | 148 | 0.5260 | −0.7315 | 0.65 | 0.38 |
| Excluding Illinois ponds, depth plot | 126 | 0.3514 | −0.4915 | 0.45 | 0.42 |
| All lakes, area plot | 148 | 0.0710 | −0.1312 | 0.50 | 0.44 |
| Excluding Illinois ponds, area plot | 126 | 0.0169 | −0.0981 | 0.38 | 0.44 |

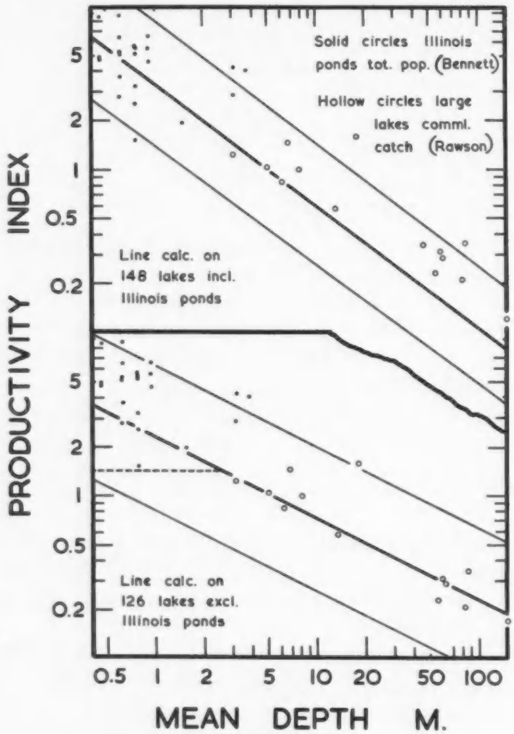


FIGURE 3.—Effect on the regression line of including the Illinois ponds (Bennett, 1943). The numbers 148 and 126 on the graph might more properly be called entries than lakes, since some lakes are entered twice (see Table III). Upper and lower lines on each graph show standard errors. Illinois ponds are entered on both plots although not used in calculating the lower one. For comparison, the large lakes discussed by Rawson (1952, 1955) are also included. They represent 25-year average commercial catches. The effects of omitting the ponds are: no effect at the 5 m. depth region where the two plots cross; diminished slope; somewhat increased error (from 0.38 to 0.42 in logs); position of ponds raised above the mean line, where they probably should be (see text); large lakes lowered to become centered on the mean line, where they probably should be. Dotted line at left of lower graph shows how allowance might be made for an absence of depth effect in very shallow ponds.

Without these Illinois ponds, Rounsefell's standing crop regression would have lost its meaning (Carlander, 1955). By the method of this paper, slopes are highly significant with or without them (Table VI). A more important question is whether a large group of unusually fertile ponds should properly be allowed to apply a force which turns the general curve clockwise. The effect of their inclusion may be tested on the position taken by the ponds themselves, and by items at the other end of the line, namely large lakes, chiefly the Great Lakes. The lines in Figure 3 are calculated on lakes listed in the Appendix (Table VIII).

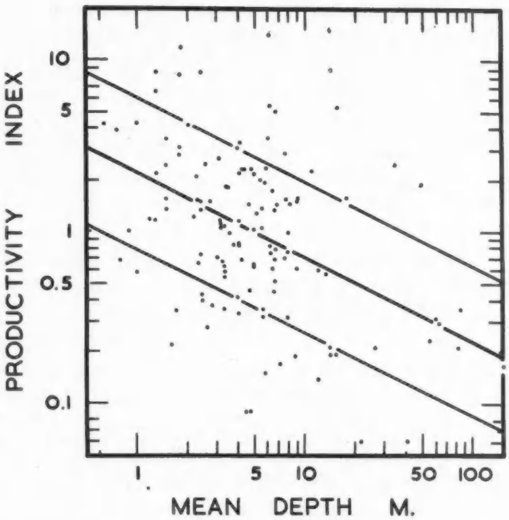


FIGURE 4.—Relation of depth to productivity index, based on 126 lakes mentioned in Table VIII (excluding only the Illinois ponds). Data on standing crop, angling catch and commercial catch are included. For the constants of this and other regressions, see Table VI.

In deciding between the representations in Figure 3, two considerations might enter. First, the Illinois ponds, being unusually fertile, ought to be above the regression line (except for Waltonian Pond in the Ozarks). Second, the largest, or rather deepest lakes, having a varied drainage basin, ought to center on the line. The records for commercial catch, as used for these lakes, are the best of the whole, nearly all being 25-year averages and some 50-year averages. The upper part of Figure 3 looks wrong by the standards just mentioned, the ponds being on the line and the lakes above it, the results of rotation caused by inclusion of the ponds in the calculation. The lower graph has a more reasonable appearance.

It is concluded that in a general line relating depth to productivity, inclusion of the Illinois ponds would produce an undesirable bias. They have therefore been omitted from construction of Figure 4 and consequently do not influence the calculation of the quality index described below.

### Calculation of a Quality Index by Which to Compare Lakes

The proposed methods of treating fish records have already been described. The lakes and ponds considered are given in the Appendix (Table VIII). The list was based on that of Rounsefell (1946), supplemented by later reports. Rounsefell omitted certain lakes and ponds from consideration for various reasons, and they are also omitted from Table VIII; so are later records where the same reasons apply. Obviously where data on area and depth are lacking no use can be made of a population study. Farm fish ponds and other such artificial situations, where stocking (generally accompanied by fertilization) is carried out, and a crop is taken during the same year, are omitted, as are artificial lakes which are drained at intervals to remove unwanted fish. A very brief creel census is not considered reliable, nor is a very small sample in a capture–mark–recapture test.

It has been necessary to re-examine most sources in Rounsefell's list in order to obtain the weights by species. Where numbers are given they have, when possible, been converted to weights by factors, usually from Carlander (1950, 1953). Rounsefell's values for area or catch are occasionally changed, where a later paper or a private communication gives supplementary records. Sometimes his catch figure is retained despite a later one, as where an author states that wartime conditions have diminished angling, etc.

In earlier estimates of total population poisoning was usually resorted to, and the lakes were often selected because of abnormal fish population or species dominance. Losses due to the sinking of some of the poisoned fish could not always be allowed for. Later estimates are often by the capture–mark–recapture technique, and generally include only legal-sized fish, or at any rate not all the small fish. According to Carlander (1955) standing crop estimates derived by draining and those by poisoning appear to be alike, while marking and recovery estimates tend to be lower. In the present analysis minnows and certain species not taken by anglers are omitted from total population estimates, a procedure which should operate to remove discrepancy.

Table VIII is a compilation of pertinent data on lake production. It shows the *productivity index*, PI, basis for its calculation and finally a *quality index*. This last, called QI, is intended to screen the effect of depth out of the productivity index and show the inherent capacity of the lake, or ideally of its drainage basin. QI purports to show what a lake of mean depth 5 m. would be expected to support under the local conditions. Five metres was chosen as the standard depth for the following reasons. First, it is practically where the line of Figure 4 crosses unit PI (actually at 5.19 m.). Thus the QI values vary around unity, a convenient number to think about. Second, the two regression lines of Figure 3 cross at close to 5 m. (actually 5.34 m.). Thus for a lake of this depth it makes

no difference whether the Illinois ponds are included or not. Third, the logarithmic mean value of the depths of lakes used to construct Figure 4 is just about 5 m. (actually antilog 0.6957 gives 4.95 m.). In other words 5 m. is the centre about which the line of Figure 4 revolves, so that any improvements in the construction of the line which might result from additional observations, would exert less change in QI at 5 m., than in a QI for some other depth. If it is desirable that QI represent a minimal adjustment of the PI, 5 m. will serve fairly well. At this depth, of course, the values are identical. For 55 of the lakes listed in Table VIII the two differ by 20% or less.

The quality indices shown in Table VIII have been calculated by the formula:

$$\log \mathrm{QI} = \log \mathrm{PI} + 0.4915(\log m - 0.6990)$$

where $m$ is the mean depth in metres.

Actually the line of Figure 4 has not sufficient basis to warrant so exact a slope designation as —0.4915. If the nearest round figure is taken, the slope becomes —0.5 and, by the use of this number, the quality index becomes a very simple concept, namely

$$\mathrm{QI} = \mathrm{PI}\sqrt{\frac{m}{5}}$$

By the use of this formula, any QI can be obtained in a few seconds. (I am indebted to Dr. M. L. Cameron for the suggestion of this simplification.)

### Theoretical Equation for Effect of Dimensions on Productivity

It is of interest to attempt a theoretical description of productivity in terms of size. The method used will be to match the conversion factors from PI to QI as given by the expression $\sqrt{m/5}$ without making use of catch data.

Consider a lake as being of any regular shape, say a cone. It is so shallow in proportion to area that the surface can be taken as equivalent to the bottom. The delivery of nutrients into the lake by regeneration from bottom deposits may be taken as proportional to the area, being a surface phenomenon. Presumably any nutrients which may be delivered with rain water will also be proportional to area. On the other hand the concentration of nutrients in the water will be inversely proportional to the volume into which they are dispersed, i.e. to the cube of the mean depth, $m$. Thus the concentration of nutrients that an algal cell has available to it, for its efforts to divide as often as possible, are related to the value:

$$\frac{\text{area}}{m^3} = c, \text{ a correction factor.}$$

The relation between area and depth is shown in Figure 2. In the central portion, excluding the first five and the last two groups, it is:

$$\log \text{area} = \frac{\log \text{depth} - 0.7392}{0.3177}$$

An extrapolation of the relationship into the shallower ponds is probably justified, since Figure 2 at the left probably suggests merely that limnologists tend to ignore shallow ponds, not that such ponds do not exist.

To the right of Figure 2 the slope changes at some 200 km.$^2$ and 30 m. depth. It is certain that the change is not sudden, as shown, but curves around a corner, and thus begins its effect below 30 m. depth. However, up to some point, say 20 m. depth, the central linear relation should be valid.

If we use the above equation to obtain a series of areas, each corresponding to a mean depth, then divide each area by the cube of its depth, factors are obtained by which to allow for the effect of dilution on productivity.

The second element determining productivity has to do with the volume of water which lies below the photosynthetic zone. The volume of a lake, on any assumption of symmetry, is proportional to the total depth cubed. Similarly the volume of some deep part, say the part below the light zone will be, like that of the tip of a cone, proportional to its depth cubed (or height from the bottom). Thus if we had a lake of total depth $p$, and depth to which plants could flourish $q$, the fraction occupied by plants would be:

$$\frac{p^3 - (p - q)^3}{p^3}$$

The next step, of course, is to combine the allowance for area with the allowance for light penetration, and so obtain a composite effect of depth on productivity, which, in suitable units, is equal to

$$c\left(\frac{p^3 - (p - q)^3}{p^3}\right)$$

We are not provided with a value for $q$, which is the depth for photosynthesis. It is known to be of the order of a few metres, and by trial and error a $q$ value can be put into the expression, so as to give results closest to those observed. (The latter are in the form of factors by which to correct the productivity at any $m$ value back to what it would be at 5 m. mean depth being, as already mentioned, $\sqrt{m/5}$.) Thus we have two further operations with the theoretical expression. First adjust it to what it would be if a mean depth of 5 m. were called unity (the $\sqrt{5/5}$ being unity). Second take the reciprocal. The results will then be comparable with observed or $\sqrt{m/5}$ values.

*Example*: Take a lake of mean depth 5 m. (maximum depth 11.75 m.).

$$\text{Log area} = \frac{\log 5 - 0.7392}{0.3177},$$

so that the area is 0.747 km.$^2$. The correction factor, $c$, is obtained by area over depth cubed:

$$c = \frac{0.747}{5^3} = 5.98 \times 10^{-3}$$

Taking 5.88 m. for a trial depth, $q$, to which plants can flourish, the fraction of the total volume of the lake in which productivity could be initiated is:

$$\frac{11.75^3 - (11.75 - 5.88)^3}{11.75^3} = 0.875$$

The last number is multiplied by the correction factor:

$$0.875 \times 5.98 \times 10^{-3} = 5.23 \times 10^{-3}$$

For purposes of comparison with observed factors, the final value, $5.23 \times 10^{-3}$, is called unity, and values for other depths are brought into relation to unity by dividing them into $5.23 \times 10^{-3}$.

To illustrate this last, take a lake of mean depth 10 m. (max. depth 23.5 m.).

$$\text{Log area} = \frac{\log 10 - 0.7392}{0.3177},$$

so that the area is 6.62 km.$^2$.

$$c = \frac{6.62}{10^3} = 6.62 \times 10^{-3}$$

The fraction for photosynthesis is:

$$\frac{23.5^3 - (23.5 - 5.88)^3}{23.5^3} = 0.580$$

and $0.580 \times 6.62 \times 10^{-3} = 3.84 \times 10^{-3}$.

Finally, to produce a number used in construction of the heavy line of Figure 5:

$$\frac{5.23}{3.84} = 1.36.$$

Looking now at Figure 5 it will be noticed that all lines cross unity at 5 m. depth (being made to do so as in the first half of the above example). The value of the heavy line at 10 m. depth is 1.36 as derived in the second part of the example. Other points to locate the lines were similarly obtained.

In Figure 5 the points are observed, being $\sqrt{m/5}$. Three lines based on the equation are calculated, using assumed trophic depths of 2.35, 5.88 and 9.40 m. The mean depth of lakes which had the above values as total depths, would be respectively 1.0, 2.5 and 4.0 m. Inspection of Figure 5 shows that for mean depths greater than 5 m. the centre line is closest to the observed points. The conclusions are: the photosynthetic zone, on this theoretical basis appears to extend down some 5.88 m., i.e. to the bottom of a lake of 2.5 m. mean depth; hence in correcting from PI to QI no further allowance need be made for shallowness at depths less than the above; in other words, any lake of mean depth less than 2.5 m. should be treated as though it were of that depth.

There are some difficulties. First, for reasons already suggested, the theoretical and observed curves deviate at depths beyond 20 m. Second, the theoretical factor at less than 5 m. is smaller than the observed one, tending to flatten out at 0.95. If these inadequacies did not exist the theory would carry more conviction. Imperfect though it is, it perhaps suggests that we are on the right track and may serve as a stimulus to someone else to provide a better explanation.

Others might approach the theory in a quite different way. For instance Carlander (1955) says, "there is no exact information on relative effort (per acre) . . . but in general it could be expected to decrease with size". To the

writer, a consideration of sea fisheries does not suggest that the distance of fishing grounds from land has very much bearing on the catch. Incidentally, the introduction into the equation above, of a term for decrease of effort with increase in lake size, diminishes the agreement between theory and observation.

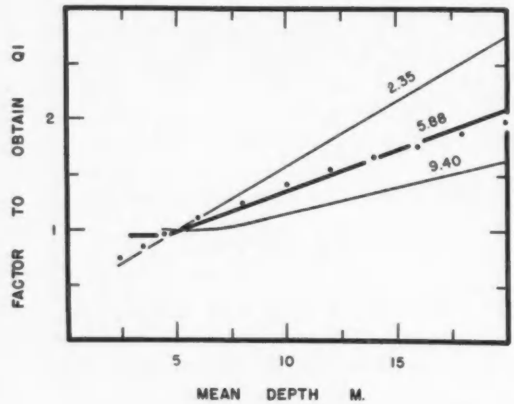


FIGURE 5.—Effect of dimensions on factor to convert PI to QI. Points are observed factors, being $\sqrt{m/5}$. Lines are theoretical, being calculated on the assumption that productivity is proportional to:

$$\frac{\text{area}}{\text{depth}^3}$$

and provided that the cycle of production can be initiated only to a certain depth to which light can penetrate in sufficient amount to support photosynthesis. The assumed depths are written on the lines, being 2.35, 5.88 and 9.40 m. It is seen that an assumed depth of 5.88 m. fits the observed points best. An average lake of 5.88 m. total depth would have a mean depth of 2.5 m.

## III. BOTTOM FAUNA

The possible relation of bottom fauna to depth has been examined by several authors, especially by Deevey (1941). He made a plot of the relation for 116 lakes over the world. The result resembled an hyperbola, with the North German lakes along the Y-axis, the Alpine lakes and other deep lakes along the X-axis (low productivity) and the remaining lakes considered, in the corner. (Molluscs were not subtracted.) Deevey was unable to find a function to describe the relation between the data and concluded that there was only "a pseudo-hyperbolic relation based on non-correlation".

As between regions of the world, even with allowance for molluscs, Deevey saw no relation between primary typology and the standing crop of the benthic

zone. Thus Connecticut, mesotrophic from the standpoint of hypolimnetic oxygen deficit, is no less productive of bottom fauna than eutrophic North Germany.

Dr. Deevey has been kind enough to supply me with his original records from an extensive literature survey. Following his suggestions, enquiries have elicited additional depths to match faunal reports which, together with more recent published information, have brought the number of lakes up to 251. On this basis a re-examination of the question is attempted.

As very few lakes have estimates of productivity based on both fishes and bottom fauna, it has not been possible to seek a relation between those two. Nor is there information known to the writer, on which to separate the species making up the bottom fauna into trophic levels, as has been done for fish. Doubtless there are biologists with sufficient knowledge to do this, and it might lead to considerable clarification.

In most regions of the world which are beset with lakes, the country is not very fertile and the water is often neutral or acid. Under such conditions few or no molluscs are likely to occur in the bottom fauna. Even in alkaline lakes the strong mollusc population does not extend to any great depth. In the shallow parts of alkaline lakes there may be many molluscs, and when a bottom fauna estimate is an average of dredgings across a lake, whether weighted for bottom segment areas or not, the mollusc shells are likely to dominate. Two examples will illustrate. In the North German lake, Dratzig (Südteil), the bottom fauna was 3493 kg. per ha. fresh weight; after subtraction of molluscs it was 33 (Lundbeck, 1926). In Schlein Lake in the Alpine region the values were respectively 5738 and 93 (Lundbeck, 1936b). Thus it would be quite hopeless to attempt a comparison of lakes without making allowance for the occasional occurrence of masses of mollusc shells. The best practice would probably be to subtract the shells from the total. but retain their living contents. However, shells and contents are not generally separated in reports, so what has been done is simply to subtract molluscs.

Another problem is how best to average samples taken at different depths. There is no systematic relation of depth to mass of bottom fauna. Sometimes the shallows are maximal, sometimes the deepest parts and sometimes an in-between level. Most reports have simply taken the average of all depths to yield the general figure for the lake. Theoretically a mean, weighted for the area at each sampling depth, would be better. Alternatively perhaps the shallows should be ignored. This is, to some extent, done when molluscs are subtracted, as they abound in the shallows.

For a considerable number of the lakes, where information was available, a weighted mean was compared to a simple mean of depths. The former was obtained by considering the lake as sections of a right cone with each section centering on the sampling depth. Each sample was adjusted to the bottom area of its section. It was found, rather surprisingly, that the two means rarely differed by as much as 20%, and the difference might be in either direction. As 20% is negligible in the present discussion, the correction efforts were not pursued, and generally the quoted averages are as provided by an author. Before making the comparison just mentioned, molluscs were subtracted.

Table VII is a summary of the results, arranged by regions. Comparing the depths with production, it is clear that no systematic trend is visible. Even if weighted for numbers of lakes, as though each lake were plotted, there is no regional trend related to depth. A reasonable interpretation is that two groups exist, the first taking in Finland, Russia, Sweden, and New Brunswick, Canada,

TABLE VII.—Summary of bottom fauna of 251 lakes by regions. Bottom fauna is given as fresh weight after subtraction of molluscs, or in a few cases, mollusc shells. In half or more of the regions there were no molluscs. In a few lakes only dry weights were given; these have been factored to fresh weight.

| Region | Number of lakes | Average mean depth | Average bottom fauna | References |
|---|---|---|---|---|
| | | *m.* | *kg. per ha.* | |
| Alpine | 43 | 44.7 | 76.1 | Lundbeck, 1936a, 1936b |
| North Germany | 64 | 7.9 | 115.0 | Lundbeck, 1926, 1933, 1936b |
| North Canada largely | 13 | 58.6 | 88.9 | Rawson, 1953<br>Deevey, 1955 |
| U.S.A., largely Conn. & N.Y. | 38 | 5.6 | 87.2 | Deevey, 1941<br>Wohlschlag, 1950 |
| Finland | 75 | 5.2 | 23.6 | Järnefelt, 1955 |
| Sweden | 5 | 13.5 | 31.1 | Deevey, 1955 |
| Russia | 10 | 4.0 | 41.3 | Deevey, 1955 |
| New Brunswick | 3 | 3.6 | 25.2 | Smith, 1952 |

which have low values, probably indistinguishable from each other. The remaining regions have high weights of bottom fauna, also, in view of the scatter, indistinguishable from each other.

As a check on the examination by regions, the lakes have been grouped and their productivity plotted in relation to depth, the result being shown in Figure 6. Only the higher productivity regions have been included, being the top four entries in Table VII. As stated in the previous paragraph, no significant difference exists between the average bottom fauna of the regions. The 158 lakes involved can thus be appropriately combined for a study of possible depth effect. Inspection of Figure 6 reveals an undulating line, which, as a whole, fails to exhibit a relation between depth and mass of bottom fauna. By making arbitrary breaks at about 5, 11 and 70 *m.*, a W-shaped line could be drawn on the figure. Some of the limbs would have a significant slope. However, such dividing up of the depth scale would hardly be justified unless one were prepared to give meanings, limnological or otherwise, to the changing slopes, which the writer cannot do. Plots with a considerable number of points can generally be treated piecemeal.

The regions which have been omitted from Figure 6 include chiefly shallow lakes. Their inclusion would operate to pull down the points at the left, and to add some additional low points there. The conclusion would be unchanged.

The largest single group of lakes, those of Finland, has also been subjected to examination similar to that shown in Figure 6. There is no trend of productivity in relation to depth.

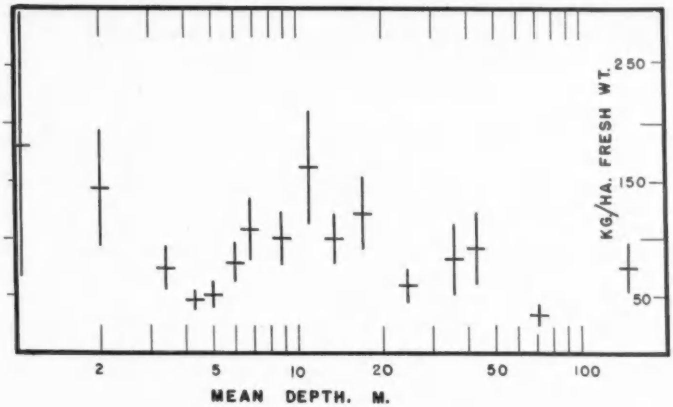


FIGURE 6.—Effect of depth on fresh weight of bottom fauna (excluding molluscs). The lakes used numbered 158, from the Alps, North Germany, Northern Canada, and the U.S.A. (see Table VII). Each point represents the average of 6 to 16 lakes of similar depth, the mean group being 10 lakes. The length of each vertical line is the standard error of the mean. No consistent relation between bottom fauna and depth can be demonstrated.

The conclusions, then, which were drawn by Deevey, are confirmed. Perhaps they are also strengthened by the inclusion of additional lakes and a somewhat different treatment of the data.

## IV. ACKNOWLEDGMENTS

A good many of the calculations have been carried out by Miss Jean A. Knowles to whom my best thanks are due.

There were many lakes for which fish production was given but for which dimensions were lacking. Through correspondence with colleagues, supplementary information has been furnished which made it possible to bring these lakes into consideration. I wish to thank particularly Messrs. G. W. Bennett, B. Curtis, S. Eddy, D. G. Frey, R. C. Holloway, N. V. Martin, D. S. Rawson, M. W. Smith, H. S. Swingle, C. M. Tarzwell, C. M. Taube, E. H. Vestal.

My obligation to Dr. E. S. Deevey, Jr., in sending his original compilation on bottom fauna has already been mentioned. Prof. H. Järnefelt very kindly provided depths of Finnish lakes, revised the Deevey lists with later information where available, and furnished records on additional lakes.

Grateful acknowledgment is made of the continued support of the work in this laboratory by the Nova Scotia Research Foundation and the National Research Council of Canada.

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# APPENDIX

TABLE VIII.—Supporting capacity of North American lakes for fish. The productivity index is obtained by dividing the crop in kg. per ha., or some part of the crop, by the appropriate factor, as obtained from Table I. Where there are species in more than one group there will be more than one productivity index, the largest being the one accepted. The group used for calculating the index is given for each lake. The quality index, QI, is obtained by multiplying the productivity index by the $\sqrt{m/5}$. QI screens out the effect of lake depth on productivity and shows the intrinsic supporting capacity of the drainage basin. It is so derived that the values fluctuate around a central value of unity. For reasons given in the text, lakes of mean depth less than 2.5 m. have been factored as though they were of that depth, i.e. the stimulating effect of shallowness is considered to have reached its maximum by 2.5 m.

| Name of lake or pond | Area $km.^2$ | Mean depth $m.$ | Productivity index: Standing crop | Productivity index: Angling catch | Productivity index: Comml. catch | Group for calc. index | Quality index QI | Reference |
|---|---|---|---|---|---|---|---|---|
| GREAT LAKES | | | | | | | | |
| (Areas × $10^4$) | | | | | | | | |
| Erie | 2.58 | 17.7 | ... | ... | 1.57 | 4 | 2.92 | Rawson '52 |
| Huron | 5.96 | 59.4 | ... | ... | 0.31 | 4 | 1.05 | do |
| Michigan | 5.80 | 84.2 | ... | ... | 0.35 | 4 | 1.40 | do |
| Ontario | 1.95 | 80.5 | ... | ... | 0.21 | 4 | 0.82 | do |
| Superior | 8.24 | 148.6 | ... | ... | 0.17 | 4 | 0.90 | do |
| CANADA | | | | | | | | |
| NOVA SCOTIA | | | | | | | | |
| Boar's Back | 0.23 | 2.6 | 0.28 | ... | ... | 3 | 0.20 | Smith '38 |
| Copper | 0.22 | 5.6 | 0.36 | ... | ... | 3 | 0.38 | Hayes & Livingstone '55 |
| do | 0.22 | 5.6 | ... | 0.32 | ... | 3 | 0.34 | Smith '52 and above |
| Jesse | 0.18 | 2.4 | 0.74 | ... | ... | 3 | 0.53 | Smith '38 |
| McCormick | 0.02 | 1.0 | 0.59 | ... | ... | 3 | 0.42 | M'Gonigle & Smith '38 |
| Sutherland | 0.41 | 2.2 | ... | 1.23 | ... | 3 | 0.87 | Smith '52 |
| Tedford | 0.21 | 2.4 | 1.38 | ... | ... | 3 | 0.98 | Smith '38 |
| NEW BRUNSWICK | | | | | | | | |
| Bonaparte | 0.43 | 7.0 | ... | 0.17 | ... | 3 | 0.20 | Smith '52 |
| Crecy | 0.20 | 2.4 | ... | 0.40 | ... | 3 | 0.28 | do |
| Gibson | 0.24 | 4.0 | ... | 0.34 | ... | 3 | 0.31 | do |
| Johnson | 0.15 | 5.8 | ... | 0.15 | ... | 3 | 0.16 | do |
| Kerr | 0.73 | 4.7 | ... | 0.09 | ... | 3 | 0.09 | do |
| Limeburner | 0.55 | 4.4 | ... | 0.09 | ... | 3 | 0.08 | do |
| St. Patrick | 0.31 | 3.3 | ... | 0.36 | ... | 3 | 0.30 | do |
| Welch | 0.18 | 2.4 | ... | 0.43 | ... | 3 | 0.31 | do |
| PRINCE EDWARD ISLAND | | | | | | | | |
| Montague | 0.09 | 2.4 | ... | 8.70 | ... | 3 | 6.18 | Smith '52, '54 |
| Southport | 0.01 | 1.3 | 6.88 | ... | ... | 3 | 4.88 | Smith '55 Priv. Comm. |
| do | 0.01 | 1.3 | ... | 8.72 | ... | 3 | 6.19 | do |
| ONTARIO | | | | | | | | |
| Glen Major | 0.03 | 1.8 | ... | 8.34 | ... | 3 | 5.92 | Harkness '41 |
| Nipigon | $4.86\times10^3$ | 54.9 | ... | ... | 0.23 | 4 | 0.74 | Rawson '52 |
| Opeongo | 52.00 | 20.8 | ... | 0.06 | ... | 3 | 0.12 | Fry '49 |
| Pearen's | 0.05 | 1.8 | ... | 11.92 | ... | 3 | 8.46 | Harkness '41 |
| Redrock | 3.00 | 7.8 | ... | 0.32 | ... | 3 | 0.40 | Fry '39 |
| St. Clair | $1.19\times10^3$ | 3.1 | ... | ... | 1.23 | 4 | 0.97 | Rawson '52 |
| Whitegull | 0.50 | 6.4 | ... | 0.45 | ... | 3 | 0.51 | Fry '39 |
| Lake of the Woods | $3.57\times10^3$ | 7.9 | ... | ... | 1.00 | 4 | 1.25 | Rawson '52 |
| MANITOBA | | | | | | | | |
| Dauphin | 518.00 | 1.5 | ... | ... | 2.48 | 4 | 1.76 | Cunningham '36 |
| Manitoba | $4.71\times10^3$ | 4.9 | ... | ... | 1.04 | 4 | 1.03 | Rawson '52 |
| Winnipeg | $22.87\times10^3$ | 13.1 | ... | ... | 0.58 | 4 | 0.93 | do |
| Winnipegosis | $5.40\times10^3$ | 6.1 | ... | ... | 0.84 | 4 | 0.93 | do |

TABLE VIII *continued*

| Name of lake or pond | Area *km.*² | Mean depth *m.* | Productivity index: Standing crop | Angling catch | Comml. catch | Group for calc. index | Quality index QI | Reference |
|---|---|---|---|---|---|---|---|---|
| SASKATCHEWAN | | | | | | | | |
| Athabaska | 8.00×10³ | 25.9 | ... | ... | 0.21 | 4 | 0.47 | Rawson '47 |
| Lac La Ronge | 1.30×10³ | 14.0 | ... | 0.19 | ... | 3 | 0.32 | Rawson & Atton '53 |
| do | do | 14.0 | ... | ... | 0.21 | 4 | 0.35 | do |
| ALBERTA | | | | | | | | |
| Beaver | 0.36 | 0.64 | ... | 4.36 | ... | 3 | 3.10 | Rawson '41 |
| Great Slave | 27.20×10³ | 62.2 | ... | ... | 0.29 | 4 | 1.00 | Rawson '52 |
| Lesser Slave | 1.19×10³ | 6.7 | ... | ... | 1.44 | 4 | 1.66 | do |
| Maligne | 21.70 | 40.2 | ... | 0.06 | ... | 3 | 0.17 | Rawson '41 |
| Pigeon & Wabamum | 100.00 | 4.5 | ... | ... | 2.36 | 4 | 2.24 | Miller '47 |
| Pyramid | 1.30 | 8.7 | 0.61 | ... | ... | 3 | 0.80 | Rawson & Elsey '50 |
| do | 1.30 | 8.7 | ... | 0.19 | ... | 3 | 0.25 | do |
| BRITISH COLUMBIA | | | | | | | | |
| Paul | 4.00 | 34.2 | ... | 2.45 | ... | 3 | 6.30 | Rawson '34; Larkin *et al.* '50 |
| U.S.A. | | | | | | | | |
| CALIFORNIA | | | | | | | | |
| Clear | 161.90 | 6.5 | ... | 0.70 | ... | 2 | 0.80 | Murphy '51 |
| do | 161.90 | 6.5 | ... | ... | 0.54 | 4 | 0.62 | do |
| Frog | 0.12 | 5.9 | ... | 2.38 | ... | 3 | 2.58 | Curtis '41 |
| June | 1.25 | 14.3 | ... | 8.79 | ... | 3 | 14.77 | do |
| Salt Springs Valley Res. | 3.64 | 3.7 | 0.87 | ... | ... | 1 | 0.77 | Wohlschlag & Woodhull '53 |
| Searsville | 0.17 | 2.0 | 4.21 | ... | ... | 2 | 2.99 | Wohlschlag '52 |
| FLORIDA | | | | | | | | |
| Big Prairie | 0.02 | 0.8 | 0.69 | ... | ... | 3 | 0.49 | Meehean '42 |
| Buck | 0.07 | 3.2 | 0.68 | ... | ... | 3 | 0.54 | do |
| Clearwater | 0.10 | 1.6 | 0.33 | ... | ... | 2 | 0.23 | do |
| First | 0.03 | 1.3 | 1.20 | ... | ... | 3 | 0.85 | do |
| Little Steep | <0.01 | 1.3 | 2.24 | ... | ... | 3 | 1.59 | do |
| ILLINOIS | | | | | | | | |
| Black Jack | 0.02 | 0.8 | 3.21 | ... | ... | 2 | 2.29 | Bennett '43 |
| Buck's | 0.04 | 0.5 | 8.61 | ... | ... | 1 | 6.11 | do |
| Crystal | 0.03 | 0.5 | 4.88 | ... | ... | 1 | 3.46 | do |
| Crystal Lake Club | <0.01 | 0.8 | 5.57 | ... | ... | 2 | 3.95 | do |
| Delta | <0.01 | 0.8 | 5.18 | ... | ... | 3 | 3.68 | do |
| Duck Island Farm | 0.02 | 1.5 | 1.94 | ... | ... | 1 | 1.38 | do |
| Duck | 0.01 | 3.1 | 4.20 | ... | ... | 1 | 3.32 | do |
| Edwards | <0.01 | 0.6 | 8.74 | ... | ... | 2 | 6.21 | do |
| Farmer City | <0.01 | 0.6 | 2.78 | ... | ... | 1 | 1.97 | do |
| Fork | <0.01 | 0.9 | 6.56 | ... | ... | 2 | 4.66 | do |
| Homewood | 0.01 | 0.6 | 5.15 | ... | ... | 2 | 3.66 | do |
| Jack's | <0.01 | 0.6 | 3.67 | ... | ... | 2 | 2.61 | do |
| Kline's | <0.01 | 0.9 | 5.53 | ... | ... | 2 | 3.93 | do |
| Lower Twin | <0.01 | 0.6 | 6.44 | ... | ... | 2 | 4.57 | do |
| Onized | <0.01 | 0.9 | 4.58 | ... | ... | 3 | 3.25 | do |
| Shell | <0.01 | 0.8 | 5.54 | ... | ... | 2 | 3.93 | do |
| Sportsmen's | 0.02 | 3.7 | 4.01 | ... | ... | 3 | 3.53 | do |
| Southside Country Club | 0.03 | 0.6 | 4.53 | ... | ... | 1 | 3.22 | do |
| Triangle | 0.01 | 3.1 | 2.86 | ... | ... | 2 | 2.26 | do |
| Upper Twin | <0.01 | 0.5 | 4.67 | ... | ... | 2 | 3.32 | do |
| Waltonian | <0.01 | 0.8 | 1.51 | ... | ... | 2 | 1.07 | do |
| Weldon Springs | 0.05 | 0.8 | 2.54 | ... | ... | 1 | 1.80 | do |

TABLE VIII *continued*

| Name of lake or pond | Area $km.^2$ | Mean depth *m.* | Productivity index: Standing crop | Productivity index: Angling catch | Productivity index: Comml. catch | Group for calc. index | Quality index QI | Reference |
|---|---|---|---|---|---|---|---|---|
| INDIANA | | | | | | | | |
| Foots | 0.19 | 0.9 | 1.04 | ... | ... | 2 | 0.74 | Lagler & Ricker '43 |
| Jasper-Pulaski Pit | <0.01 | 4.0 | 3.05 | ... | ... | 2 | 2.75 | Ricker '42 b |
| Muskellunge | 0.12 | 2.4 | ... | 1.53 | ... | 2 | 1.09 | Ricker '45 |
| Oliver | 1.44 | 11.8 | ... | 0.14 | ... | 3 | 0.21 | Gerking '50 |
| Shoe | 0.17 | 4.1 | 3.30 | ... | ... | 2 | 3.00 | Ricker '42 a |
| do | 0.17 | 4.1 | ... | 2.24 | ... | 2 | 2.04 | do |
| Springwood | 0.04 | 1.0 | 4.42 | ... | ... | 2 | 3.14 | Ricker '42 b |
| Yellowwood | 0.59 | 4.1 | ... | 0.70 | ... | 3 | 0.64 | Ricker '45 |
| IOWA | | | | | | | | |
| Lost Island | 5.1 | 1.5 | ... | 3.56 | ... | 2 | 2.53 | Rose & Moen '51 |
| MICHIGAN | | | | | | | | |
| Airport | 0.03 | 3.6 | 1.00 | ... | ... | 3 | 0.85 | Ball '48 |
| Booth | 0.07 | 4.0 | 0.87 | ... | ... | 3 | 0.78 | do |
| Burke | <0.01 | 7.5 | 0.71 | ... | ... | 3 | 0.87 | do |
| Cedar | 0.23 | 3.5 | ... | 1.85 | ... | 3 | 1.55 | Hazzard & Eschmeyer '38 |
| Clear | 0.55 | 3.6 | ... | 1.85 | ... | 3 | 1.57 | do |
| Clear | 0.05 | 1.2 | 1.22 | ... | ... | 1 | 0.87 | Eschmeyer '38 c |
| Crooked | 0.28 | 2.6 | ... | 2.49 | ... | 3 | 1.82 | Hazzard & Eschmeyer '38 |
| Deep | 0.06 | 7.8 | 0.77 | ... | ... | 3 | 0.95 | Carbine & Applegate '48 |
| Doyle | 0.04 | 1.8 | ... | 3.17 | ... | 3 | 2.25 | Hazzard & Eschmeyer '38 |
| East Fish | 0.06 | 5.5 | 1.38 | ... | ... | 3 | 1.44 | Ball '48 |
| Fife | 2.30 | 5.1 | 1.29 | ... | ... | 3 | 1.30 | Cooper '52 |
| do | 2.30 | 5.1 | ... | 2.19 | ... | 3 | 2.21 | Eschmeyer '36, '37, '39 |
| Fitzek | 0.03 | 6.5 | 1.34 | ... | ... | 3 | 1.53 | Greenbank '41 |
| Ford | 0.04 | 4.3 | 2.38 | ... | ... | 3 | 2.21 | Eschmeyer '38 b, c |
| Hemlock | 0.02 | 8.2 | ... | 1.47 | ... | 3 | 1.87 | Eschmeyer '38 a |
| Howe | 0.05 | 3.1* | 1.12 | ... | ... | 3 | 0.88 | Eschmeyer '38 c |
| Holland | 0.02 | 2.8 | 0.38 | ... | ... | 2 | 0.29 | Ball, '48 |
| Kimes No. 3 | 0.03 | 2.3 | 2.12 | ... | ... | 3 | 1.51 | do |
| Linnbeck | 0.02 | 3.3 | 0.56 | ... | ... | 3 | 0.46 | do |
| Lost | 0.02 | 6.7 | ... | 5.00 | ... | 3 | 5.78 | Eschmeyer '38 a |
| Mill | 0.83 | 3.3 | ... | 1.12 | ... | 2 | 0.92 | Hazzard & Eschmeyer '38 |
| North Basin Twin | 0.03 | 7.8 | 1.56 | ... | ... | 2 | 1.93 | Ball '48 |
| O'Brien | 0.04 | 3.9 | 0.42 | ... | ... | 3 | 0.37 | do |
| Pike No. 4 | 0.02 | 2.3 | 1.57 | ... | ... | 3 | 1.11 | do |
| Pond Four | <0.01 | 0.8 | 4.03 | ... | ... | 3 | 2.86 | Greenbank '41 |
| Portage | 1.94 | 3.3 | ... | 0.60 | ... | 3 | 0.49 | Hazzard & Eschmeyer '38 |
| Section Four | 0.01 | 9.2 | 1.61 | ... | ... | 3 | 2.17 | Eschmeyer '38 b, c |
| South Twin | 0.02 | 5.5 | 2.01 | ... | ... | 3 | 2.10 | do '38 c |
| Standard | 0.07 | 4.0 | 0.84 | ... | ... | 3 | 0.76 | do '38 c |
| Sugarloaf | 0.73 | 1.5 | 1.38 | ... | ... | 3 | 0.98 | Cooper '52 |
| do | 0.73 | 1.5 | ... | 1.57 | ... | 3 | 1.11 | Hazzard & Eschmeyer '38 |
| Swanzy | 0.08 | 5.9 | 1.94 | ... | ... | 3 | 2.10 | Ball '48 |
| Third Sister | 0.04 | 6.5 | 1.73 | ... | ... | 2 | 1.97 | Brown & Ball '43 |
| Twin | 0.09 | 11.7 | 0.63 | ... | ... | 3 | 0.96 | Ball '48 |
| Walsh | 0.04 | 2.7 | 1.55 | ... | ... | 2 | 1.15 | do |
| West Lost | 0.02 | 6.2 | ... | 5.47 | ... | 3 | 6.07 | Eschmeyer '38 a |
| MINNESOTA | | | | | | | | |
| Deer | 7.50 | 3.3 | ... | 0.64 | ... | 3 | 0.52 | Eddy '41 |
| Eighth Crow Wing | 1.99 | 5.5 | ... | 1.07 | ... | 2 | 1.12 | do |
| Island | 1.55 | 6.3 | ... | 0.62 | ... | 3 | 0.69 | do |
| Red | $1.11\times10^3$ | 4.0 | ... | ... | .86 | 4 | 0.77 | Smith *et al.* '52 |

TABLE VIII *continued*

| Name of lake or pond | Area km.² | Mean depth m. | Productivity index: Standing crop | Angling catch | Comml. catch | Group for calc. index | Quality index QI | Reference |
|---|---|---|---|---|---|---|---|---|
| MISSOURI | | | | | | | | |
| Wappapello | 23.10 | 1.7 | ... | 0.35 | ... | 2 | 0.25 | Patriarche '53 |
| OHIO | | | | | | | | |
| Alma | 0.29 | 3.0 | ... | 0.71 | ... | 2 | 0.55 | Pelton '50 |
| OKLAHOMA | | | | | | | | |
| Pawhuska | 0.38 | 9.1 | ... | 1.51 | ... | 3 | 2.02 | Thompson & Hutson '51 |
| OREGON | | | | | | | | |
| Diamond | 11.70 | 7.6 | ... | 2.85 | ... | 3 | 3.51 | Holloway '49 |
| East | 3.90 | 15.8 | ... | 5.36 | ... | 3 | 9.38 | do |
| Paulina | 5.30 | 49.3 | ... | 1.89 | ... | 3 | 5.84 | do |
| South Twin | 0.53 | 6.1 | ... | 14.24 | ... | 3 | 15.71 | do |
| TENNESSEE | | | | | | | | |
| Pickwick Reservoir | 189.00 | 6.7 | ... | ... | .79 | 4 | 0.91 | Bryan & Tarzwell '41 |
| Wheeler Reservoir | 275.00 | 4.9 | ... | ... | .65 | 4 | 0.64 | do |
| Wilson Reservoir | 62.70 | 11.0 | ... | ... | 2.23 | 4 | 3.30 | do |
| VIRGINIA | | | | | | | | |
| Claytor | 18.20 | 15.3 | ... | 0.19 | ... | 3 | 0.33 | Rosebery '51 |
| WISCONSIN | | | | | | | | |
| East Twin | 0.05 | 3.1 | 1.17 | ... | ... | 1 | 0.92 | O'Donnell '43 |
| Kegonsa | 12.70 | 4.6 | 1.47 | ... | ... | 1 | 1.41 | Hacker |
| do | 12.70 | 4.6 | ... | 0.46 | ... | 3 | 0.44 | Frey & Vike '41 |
| Long | 0.11 | 3.1 | 2.68 | ... | ... | 3 | 2.12 | O'Donnell '43 |
| Peter & Paul | 0.02 | 6.0 | 3.50 | ... | ... | 3 | 3.80 | Johnson & Hasler '54 |
| Pike & Round | 5.30 | 2.3 | ... | 0.66 | ... | 3 | 0.47 | Elkins '37 |
| Waubesa | 8.20 | 4.9 | 2.36 | ... | ... | 1 | 2.34 | Helm |
| do | 8.20 | 4.9 | ... | 0.63 | ... | 2 | 0.62 | Frey & Vike '41 |
| West Twin | 0.06 | 6.2 | 0.76 | ... | ... | 3 | 0.84 | O'Donnell '43 |
| Wingra | 0.80 | 1.8 | 2.86 | ... | ... | 1 | 2.03 | Juday '38 |

# The Molecular Nature of Organic Matter in Lakes and Oceans, with Lesser Reference to Sewage and Terrestrial Soils[1,2]

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CONTENTS



## ABSTRACT

The compounds listed below have been isolated from, or identified in, the sources under review. Where there is still some question as to the exact identity, the name of the compound is followed by a question mark. Compounds identified on the basis of inadequate data are not listed here.

*Seston* (freshwater and marine)

*Free:* aphanicin, aphanin (=myxoxanthin), arginine, biotin (?), β-carotene, choline, cystine, flavacin, fructose, glucose, hentriacontane (?), histidine, lysine, maltose, monomethylamine, niacin, sucrose, thiamin, trimethylamine, tryptophan, tyrosine, vitamin A, vitamins D, vitamins $B_{12}$.

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[2]Modified from a paper presented in a symposium on "The dynamics of the lake bottom", at the Ninth Annual Meeting of the Canadian Committee on Freshwater Fisheries Research, Ottawa, January 2, 1956.

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*In hydrolysates:*

Sugars: galactose, glucose, rhamnose, xylose.

Amino acids: α-alanine, arginine, aspartic acid, glutamic acid, glycine, histidine, hydroxyproline, leucine, phenylalanine, proline, tryptophan, tyrosine, valine.

Other compounds: aphanizophyll (=myxoxanthophyll?), astacene, cetyl alcohol, cholesterol (?), glucuronic acid, glycerol, lutein, peridinin.

*Dissolved organic matter* (freshwater and marine)

*Free:* biotin, dehydroascorbic acid, glucose, niacin (?), sucrose, thiamin, vitamins $B_{12}$.

*In hydrolysates:* α-alanine, aspartic acid, cystine, glutamic acid, glycine, histidine, tryptophan, tyrosine.

*Aquatic sediments* (freshwater and marine)

*Free:*

Sugars: arabinose, fructose, fucose, galactose, glucose, maltose, ribose, sucrose, xylose.

Amino acids: α-alanine, glutamic acid.

Carotenoids: α-carotene, β-carotene, flavorhodin (?), leprotene (?), myxoxanthin (?), rhodopurpurin (?), rhodoviolascin, torulene (?).

Other compounds: acetic acid, biotin, *n*-butyric acid, cellulose, formic acid, pentatriacontane, β-sitosterol, thiamin (?), trimethylamine, tritriacontane, vitamins $B_{12}$.

*In hydrolysates:*

Sugars: arabinose, fructose (?), fucose, galactose, glucose, mannose, rhamnose, ribose, xylose.

Amino acids: α-alanine, arginine, aspartic acid, cystine, glutamic acid, glycine, histidine, isoleucine, leucine, lysine, serine, tyrosine, valine.

Carotenoids: antheraxanthin (?), fucoxanthin (?), petaloxanthin (?), sulcatoxanthin (?), zeaxanthin (?).

Other compounds: adenine, arachidic acid, behenic acid, caproic acid, caprylic acid, cerotic acid, cytosine, galacturonic acid, guanine, heptacosanoic acid, heptacosanol, heptoic acid, montanic acid, uracil.

*Sewage and Activated Sludge*

*Free:* acetic acid, biotin, *n*-butyric acid, folic acid (?), indole (?), niacin (?), pantothenic acid (?), propionic acid, pyridoxine (?), riboflavin (?), skatole (?), thiamin, tryptophan, tyrosine, *n*-valeric acid (?), vitamins $B_{12}$.

*Terrestrial Soils*

*Free:*

Sugars: no free sugars identified.

Amino acids: α-alanine, γ-aminobutyric acid, arginine, asparagine, aspartic acid, glutamic acid, glutamine, glycine, leucine and/or isoleucine, lysine, serine, threonine, valine.

Other acids: acetic acid, acrylic acid, *p*-aminobenzoic acid (?), benzoic acid, 3,5-cresotic acid, α-crotonic acid, cyanuric acid, 8,9-dihydroxystearic acid, formic acid, α-hydroxystearic acid, lignoceric acid, oxalic acid, α-picoline-γ-carboxylic acid, saccharic acid, succinic acid.

Other compounds: adenine, allantoin, biotin, chrysene, creatinine, cytosine, hentriacontane, hypoxanthine, inositol, mannitol, methylglyoxal, niacin (?), phytin, pyridoxine (?), riboflavin (?), salicylic aldehyde, thiamin, trithiobenzaldehyde, vanillin, vitamins $B_{12}$, xanthine.

*In hydrolysates:*

Sugars: arabinose, fucose, galactose, glucose, mannose, rhamnose, ribose, xylose.

Amino acids: α-alanine, β-alanine, α-aminobutyric acid, γ-aminobutyric acid, arginine, aspartic acid, cystine (?), cysteic acid, α,ε-diaminopimelic acid, glutamic acid, glycine, histidine, hydroxyproline, isoleucine, leucine, lysine, methionine (?), methionine sulphoxide, proline, phenylalanine, serine, threonine, tyrosine, valine.

Other compounds: galactosamine, galacturonic acid, glucosamine, glucuronic acid, glycerol, guanine, inositol.

Partially characterized organic matter fractions from freshwater and marine seston, water and mud are also reviewed. Special attention is devoted to algal toxins and to the occurrence and activity of free enzymes in nature.

The number of adequately identified organic compounds in each of the sources under review is: seston, 45; water, 15; sewage, 14; aquatic sediments, 62; terrestrial soils, 76.

## INTRODUCTION

THE development of chromatographic methods of analysis during the present century has given a new perspective to the study of biochemistry. It is now possible, using chromatographic methods, to identify minute amounts of specific organic compounds even when they are present in the most complex mixtures. As yet there have been few applications of these techniques to problems of limnology and oceanography. There is, however, good reason to suspect that such application will shed new light on the hitherto little understood processes of mineralization, food cycles, plankton succession and production rates. In the past, these processes have been almost solely studied (on the chemical level) by analyses for elements or general classes of organic compounds (proximate analysis). The important point to realize is that the organism responds to the molecular configurations of atoms rather than to the atoms themselves. A particular vitamin lack is alleviated only if that vitamin or a metabolic precursor is available in the diet. It is therefore of the utmost importance, when working in the field of biochemical ecology, to have a precise knowledge of the molecular nature of the organism and its environment. Since study along these lines is just beginning to have a general interest, this seems to be an appropriate time to review the work that has already been done.

The review is specifically designed to cover the following information:

1. The isolation or identification of adequately and inadequately characterized organic compounds from the seston, water (dissolved organic matter) and sediments of lakes and oceans.
2. The isolation or identification of adequately characterized organic compounds from terrestrial soils, sewage and activated sludge.

The central part of the review is thus concerned with natural aquatic ecosystems. Data referring to sewage and terrestrial soils are included because of the comparability of these environments to their aquatic counterparts. To omit this inclusion would have been a great oversight. The reviewer feels, like Mortimer (1949), that there could be more fruitful co-operation between limnologists and soil scientists. It is hoped that this review may further such co-operation. With regard to what constitutes an "adequate characterization" of an organic compound, I have attempted to maintain a middle road between stringency and laxity. In so far as possible, the criteria for identity of each compound are given, thus permitting a personal evaluation of the work by the reader.

One should never forget that it is always wise to question whether a compound isolated from an extract actually occurred in the sample before analysis. *Isolated from* DOES NOT NECESSARILY MEAN *occurred in.* Compounds isolated by

markedly destructive techniques, e.g. pyrolysis, were purposely excluded from review. The products so isolated have little meaning in terms of the compounds originally present.

It may be well at the outset to say that my main interest in preparing this review has been in the organic constituents of sediments. The sediment is important because it is the only source of information about lakes and oceans during their long histories. There is also a great supply of marine and fresh-water sedimentary rocks on the earth's surface. Some of these are rich in organic matter (Breger, 1954). While it is not my purpose to review work on fossils and lithified sediments, it may be worth while to point out that Treib's (1936) discovery of porphyrins in oil and oil shales has been cited as providing the most conclusive proof that oil has originated under low temperature conditions in a reducing environment. Similarly, Abelson's (1954) discovery of amino acids in hydrolysates of fossil shells and bone (up to 400 million years old) has opened up new approaches to the studies of evolution, diagenesis and the origin of life.

It may appear facetious to ignore all the chemical work that has been done with pure cultures of planktonic organisms. Indeed, any compound isolated from a laboratory culture of a plankter must be expected to occur in seston if that species is present, *providing* that the compound did not arise from an adaptive enzyme system peculiar to laboratory conditions. Planktonic and other organisms spend more of their time dead than alive, and the healthy cell is the exception rather than the rule in nature. Protoplasmic constituents are thus continually undergoing modification, for the most part by bacterial breakdown. During these mineralization processes some of the constituents of healthy cells are destroyed. Others, because of their resistance to breakdown, become concentrated in the sediment. Anything may be expected to occur in seston, water and mud. The first questions are: what does occur, and in what amounts?

## MINERALIZATION

It is not my purpose here to enter into a detailed discussion of mineralization processes in natural waters, but only to point out that the studies which have been made along these lines could profitably be repeated studying the breakdown of single organic compounds. Sediment trap collections of sinking seston have been studied by Kleerekoper (1953). Kleerekoper found that most of the decomposition of seston occurred above the thermocline. The laboratory decomposition of plankton has been studied by Skopintsev and Bruk (1940), Skopintsev (1949), Rakestraw and von Brand (1947, *q.v.* for earlier work) and Waksman and Renn (1936, *q.v.* for earlier work).

The dissolved organic matter of lake and sea water occurs in concentrations higher than those of particulate organic matter (seston). Waksman and Carey (1935b) and Waksman and Renn (1936) demonstrated that the dissolved organic matter of sea water could be used as an energy source for bacteria in the laboratory. ZoBell and Grant (1943) have further shown that marine bacteria in the laboratory are capable of utilizing even smaller concentrations of organic matter than exist naturally either in fresh or salt water. It does not immediately

follow that these processes occur under natural conditions, for ZoBell (1943) and others have demonstrated that much of the bacterial activity of sea water in the laboratory is due to the influence of the containing vessels.

Pütter's hypothesis that the dissolved organic matter of water may be an important food source for multicellular animals (including fishes) has been effectively criticized and reviewed by Moore *et al.* (1912) and Krogh (1931). The hypothesis has never been rigorously tested even though excellent experimental tools are now available (isotopes, microfilters, chromatography).

The decomposition of dead seston continues after the seston has reached the mud surface. It seems remarkable that the activity of bacteria in freshwater sediments could be so great as to raise the temperature of near-surface sediments as much as 5°C. above that of the overlying water (12°C.). This was the explanation proposed by ZoBell, Sisler and Oppenheimer (1953) to account for the high temperatures of mud from Lake Mead.

## THE HUMUS FRACTIONS

The soil organic matter preparations known under the names humic acid, humin, crenic acid, aprocrenic acid, ulmic acid, ulmin and the like, are still occasionally referred to as single chemical entities, as they were thought to be during the 19th century (see Schreiner and Shorey, 1909, for an excellent review of the early work on soil organic matter). The fact is that they are little more than preparations whose composition varies with the method of isolation and the source (Schreiner and Shorey, 1909; Waksman, 1930; Broadbent, 1955). Forsyth (1946) points out that only three criteria of purity have been applied to humic acid: its solubility in base, insolubility in acid and insolubility in organic solvents. Forsyth further showed that when proximate analyses and analyses for C, H, N, and acetyl, methoxyl, hydroxyl and carboxyl groups were applied to humic acid fractions from different sources, the results were quite variable. Trojanowski (1952) and Hayashi and Nagai (1953) subjected humic acid fractions to chromatography, resolving them into several fractions which fluoresce in ultraviolet light. The humic acid fraction of marine sediments has been studied by Waksman (1933). I do not know of any serious work on the precipitated humic fractions of lake sediments.

## ELEMENTARY AND PROXIMATE ANALYSES

These methods have yielded valuable data indicating the general nature of the organic matter in natural bodies of water. Various approaches have been used. Brandt (1898) was the first to measure plankton in terms of crude protein, fat, carbohydrates and ash. Krogh and Lange (1931) and Birge and Juday (1926, 1934) later and more extensively assessed the plankton and dissolved organic matter in terms of the same fractions. The method of Birge and Juday was to subtract the weight of crude protein ($N \times 6.25$) and the weight of the ether extract ("fat") from the ash-free weight of the sample, leaving the rest as carbohydrate. The "fat" fraction was usually about 4% of the dry weight of ash-free plankton or dissolved organic matter. The rest of the organic matter from these

sources was roughly one-third crude protein and two-thirds "carbohydrate". The data of Bremner (1949) and Sowden and Atkinson (1949) show that only one-third to one-half of the soil organic-N occurs in the form of proteinaceous compounds. Konshin (1939) has shown the same for lake sediments, and Peterson, Fred and Domogalla (1925) for the dissolved organic matter of lake water. The "carbohydrate" fraction of the Birge and Juday scheme must of course include compounds other than those usually classed as carbohydrates; and the "fat" fraction, things other than glycerides.

The proximate method of analysis devised by Waksman and Stevens (1928) has been widely used in the study of soil and sediment organic matter. This method is essentially based on successive extractions of a sample with organic solvents, then water, followed by graded hydrolysis and estimation of the reducing substances so liberated to yield values for hemicelluloses and celluloses. The weight of ash- and N-free residue is calculated as lignin. As applied to lake sediments this method shows that "lignins" usually constitute 20 to 50% of the organic matter of the sediment (Kusnetzov, 1934a, 1934b; Kusnetzov and Kusnetzova, 1935; Speranskaja, 1935; Sugawara, 1939; Hutchinson and Wollack, 1940; Ponomarev, 1947). Hemicelluloses and celluloses occur in smaller amounts. Ponomarev (1947) found that roughly one-half of lake sediment hemicelluloses were pentosans. Bitumens (benzene–alcohol soluble fraction) compose 2–10% of the organic matter.

Data obtained by the proximate methods of analysis indicate that carbohydrates and proteins are the main classes of organic compounds in seston and dissolved organic matter. In the mud these are diluted to a considerable extent by fractions known as lignins and humic substances.

## CARBOHYDRATES

Sugars found in acid hydrolysates of seston, aquatic sediments and terrestrial soils are listed in Table I.

TABLE I.—Sugars in acid hydrolysates of seston, gyttja, peat and terrestrial soil.

| Source | Sugars | References |
|---|---|---|
| Seston | Glucose, galactose, rhamnose, xylose | Hough, Jones and Wadman (1952) |
| Gyttja | Fructose, glucose, galactose, xylose, ribose, arabinose | Vallentyne and Bidwell (1956) |
| Peat | Glucose (1, 3), galactose (1,3–5), fucose (2), fructose (5), mannose (1,3–5), rhamnose (1,3,4), xylose (1,3,4), arabinose (1,3,4) | (1) Black, Cornhill and Woodward (1955)<br>(2) Duff (1952b)<br>(3) Theander (1952)<br>(4) Theander (1954)<br>(5) Waksman (1942) |
| Terrestrial soil | Glucose (1,2,7), galactose (1,2,7), mannose (2,7), rhamnose (1,4,7), xylose (2,3,5,6,7), ribose (2,6,7), arabinose (2,7), fucose (2) | (1) Duff (1952a)<br>(2) Forsyth (1950)<br>(3) Schreiner and Shorey (1910a)<br>(4) Shorey (1913)<br>(5) Shorey and Lathrop (1910)<br>(6) Stevenson *et al.* (1952)<br>(7) Whistler and Kirby (1956) |

SESTON. Surprisingly little information is available about the carbohydrates of seston. Brandt (1898) reported 4.54% chitin in a collection of copepods taken from a pond near Kiel. The value is reasonable, but the purity is questionable since the datum only refers to the weight of residue left after various extractions. Schuette (1918) was unable to demonstrate reducing sugars and pentoses in water and alcoholic extracts of seston from Lake Mendota. On the other hand, Skopintsev (1948) found pentoses (positive furfural test) in the seston of river, lake and swamp waters. Skopintsev further stated that methylpentoses also occur in seston, and that they are concentrated in decomposed seston. Hough, Jones and Wadman (1952) isolated a polyglucosan of the amylopectin type from *Oscillatoria*-rich seston collected from Windermere, England. A similar collection of *Nostoc*-rich seston from the same lake yielded a complex polysaccharide composed of xylose, galactose, rhamnose, smaller amounts of glucose and an unknown sugar, and 30% uronic acids (glucuronic acid identified). It is apropos to note that Bishop, Adams and Hughes (1954) have since isolated a polysaccharide containing glucose, xylose, galactose, rhamnose, arabinose and glucuronic acid in the proportions 5:4:1:1:1:4 from a pure culture of *Anabaena cylindrica*. Whittaker and Vallentyne (1957) analysed freshwater seston for free sugars. Sucrose, maltose, glucose and fructose were found with the total concentration of free sugar amounting to about 0.4% of the dry weight of the seston.

WATER. Collier *et al.* (1953) found evidence of substances in sea water which increased the pumping rates of oysters. These substances were measured by reaction with N-ethyl carbazole, and were thought to be either carbohydrates or something closely bound to carbohydrates. Dehydroascorbic acid has been isolated in crystalline form from sea water by Wangersky (1952). Voronin (1952) interestingly reports that humic substances in inland waters destroy ascorbic acid. Wangersky (1952) also reported the presence of a "rhamnoside" in inshore water of the Gulf of Mexico. The "rhamnoside" may attain concentrations up to 0.1 g./l. Lewis and Rakestraw (1955) verified Wangersky's results on Pacific water, but found much lower concentrations ($<$ 0.7 mg./l.). Algae have been shown to liberate carbohydrates to their culture media (Krogh and Lange, 1930; Aleyev, 1934; Fogg, 1952; Lewin, 1955), but the importance of such excretion in nature has yet to be demonstrated. Vallentyne and Whittaker (1956) have recently found traces of free sucrose and glucose in filtered lake water.

SEDIMENT. It is well known from proximate analyses that both hemicelluloses and celluloses are present in sediments. In the proximate methods, hemicelluloses are differentiated from celluloses by their ease of hydrolysis, and pentosans from hexosans by the furfuraldehyde reaction of pentosans. The only reasonably well purified polysaccharide obtained from sediments is the cellulose isolated from peat by Hess and Komarewsky (1928). The cellulose was characterized by elementary analysis, polarimetry and formation of the acetate. The preparation was shown to be devoid of methoxyl groups. Other soil and sediment polysaccharides must be regarded as impure fractions, or data indicative of fractions, rather than pure compounds.

Black, Cornhill and Woodward (1955) isolated a polysaccharide fraction from peat which had an equivalent weight (assuming one uronic acid anhydride per molecule) of 3150. The components identified after hydrolysis were: glucose, mannose, xylose, galactose and an unidentified uronic anhydride in the proportions 12:3:2:1:1. Theander (1954) studied the sugars liberated by hydrolysis of water and methanol extracts of *Sphagnum* peats aged up to 4,800 years. Mannose and, to a lesser extent, rhamnose were found to be the most stable sugars during humification. Uronic acids were also found to be present: galacturonic acid and an unidentified monomethyluronic acid. Theander (1952) found evidence of methylpentoses in peat hydrolysates, but he did not identify the specific compounds. There is one report of fructose in peat hydrolysates (Waksman, 1942). All other workers report the absence of fructose in both peat and soil hydrolysates. In hydrolysates of gyttja, fructose arises solely from sucrose (Vallentyne and Bidwell, 1956).

Free sugars are reported to occur in 70% ethanol extracts of lake sediments by Vallentyne (1954) and Vallentyne and Bidwell (1956). Most workers have assumed that free sugars would be utilized by sediment microorganisms as quickly as they are liberated by decomposition processes. This assumption has been questioned by Vallentyne and Bidwell (1956) who report the following free sugars in 70% ethanol extracts of gyttja: sucrose, glucose, galactose, fructose, xylose, ribose and arabinose. Glucose was present in the largest amounts (up to 1.0 g./kg. of sediment organic matter). Galactose was present in smaller amounts and the pentoses little more than detectable. Free sucrose and free fructose were found in only one of six samples analysed. Vallentyne and Bidwell (1956) also found small amounts of free glucose in 5,000- to 9,000-year-old gyttja. Whittaker and Vallentyne (1957) have added maltose to the list of free sugars, and also shown that the concentrations of free sugars decrease with depth below the mud surface. Theander (1954) identified free sucrose, glucose and fructose in fresh *Sphagnum*, and small amounts of free fucose in both *Sphagnum* and *Sphagnum* peat.

Apparently no one has examined aquatic sediments for chitin or its hydrolytic products.

SOIL. Soil carbohydrates have been more extensively studied than those of wet sediments. Proximate analysis indicates the presence of hemicelluloses (both pentosans and hexosans), polyuronides, celluloses and other carbohydrates or carbohydrate-like material. Shorey (1913) partially purified a soil glycoside which yielded rhamnose as the sugar component on hydrolysis. Forsyth (1950) partially fractionated water-soluble polysaccharides of different soils and found them to be similar in optical rotation before hydrolysis and in the sugars released by hydrolysis. A polysaccharide (polysaccharide B) resistant to hydrolysis was isolated. It was found to have an equivalent weight of 924 (alkali titration) and liberated the following components on hydrolysis: galactose, glucose, mannose, xylose and aldobiuronic acid in the proportions 2:2:2:3:2. The aldobiuronic acid consisted of glucose bound to glucuronic acid. Forsyth failed to detect any

ketoses in hydrolysates of the water soluble polysaccharides. Whistler and Kirby (1956) have examined the hydrolytic products from water-soluble polysaccharides of American soils. The following were identified: D-galactose, D-glucose, D-mannose, L-arabinose, D-xylose, L-rhamnose, ribose (traces), glucosamine (traces), and glucuronic acid.

Duff (1952a) found evidence of monomethylhexoses in hydrolysates of soil extracts—probably methylglucose and methylgalactose. Stevenson *et al.* (1952) have partly purified a clay-adsorbed organic colloid which on hydrolysis yielded amino acids, xylose, ribose, galacturonic acid and glucurone (traces).

Chitin may be expected to occur in soil (from insects and fungi) but it has yet to be isolated as such. Although Forsyth (1950) found no evidence of hexosamines in hydrolysates of soil organic matter fractions, Bremner and Shaw (1954) reported that 5 to 10% of the soil-N occurred as glucosamine and/or galactosamine (the acetyl group lost during hydrolysis). Adams, Bartholomew and Clark (1954) found both glucosamine and galactosamine on paper chromatograms of soil hydrolysates in concentrations of approximately 30 and 10 mg./100 g. of dry soil. Whistler and Kirby (1956) detected traces of glucosamine in hydrolysates of water-soluble soil polysaccharides.

Mannitol (crystals, m.p., optical activity) was first obtained from soil by Shorey (1913), and its presence later confirmed (mixed m.p., m.p. of hexaacetate) by Sallans *et al.* (1937).

COMMENTS. There is very little that one can say in general terms from the information summarized above. The data are too varied and too fragmentary. A suggestion that ketoses are unstable in sediments and soils is perhaps the only valid conclusion. Because of the difficulty of isolating polysaccharides in pure form, and the difficulty of assessing their purity, it would seem that the most profitable studies for the present will be made on low molecular weight carbohydrates, either free or liberated by hydrolysis.

## PROTEINACEOUS COMPOUNDS

Purified proteins have not been isolated from any of the sources under review. About all that is known is that hydrolysis liberates far larger quantities of amino acids than can be detected in the free state. Very little attention has been given to the proteinaceous compounds in either lakes or oceans in spite of the early demonstration by Peterson, Fred and Domogalla (1925) that amino acids and peptides are present in the dissolved organic matter of lake water. Even seston has been little investigated. The whole question of amino acids in natural sources may be important since some organisms are unable to synthesize certain amino acids, and therefore require them preformed in the diet. Table II lists the amino acids found in hydrolysates of seston, the dissolved organic matter of lake water, freshwater sediments and soils. The occurrence of an amino acid in a hydrolysate does not necessarily mean that the amino acid occurred in peptide form. The short lists for amino acids in hydrolysates of seston, water and sediment reflect the few and incomplete studies that have been made. Apparently

no one has attempted to identify amino acids in any part of the marine ecosystem (excluding large organisms) except nannoplankton (Lasker and Lane, 1953). The list of amino acids found in soil hydrolysates shows nearly all the amino acids known from pure proteins. Tryptophan, however, is conspicuous by its absence, which may be partly due to decomposition during analysis. Schreiner and Shorey (1909) suggested that the α-picoline-γ-carboxylic acid of soils may be a tryptophan decomposition product (through kynurenic acid). The demonstration of tryptophan in the dissolved organic matter of lake water (Peterson, Fred and Domogalla, 1925) was based on colorimetric tests on crude hydrolysates. In view of the apparent absence of tryptophan from soils and aquatic sediments, its presence in the dissolved organic matter of lake water needs confirmation. Free amino acids have been found to occur in some sources. These data are referred to in the text. (See Addendum, page 82, for additional information.)

TABLE II.—Amino acids in hydrolysates of seston, water, freshwater sediments and terrestrial soil. (See Addendum, page 82, for marine sediments.)

| Source | Amino acids | References |
|---|---|---|
| Seston | α-Alanine (2,3), arginine (2), aspartic acid (2,3), glycine (2), glutamic acid (2,3), histidine (2), hydroxyproline (2), leucine (1,2), phenylalanine (2), proline (1,2), tryptophan (2), tyrosine (1,2), valine (1,2) | (1) Lasker and Lane (1953)<br>(2) Mazur and Clarke (1938)<br>(3) Vallentyne (1954) |
| Water | α-Alanine (2), aspartic acid (2), cystine (1), glutamic acid (2), glycine (2), histidine (1), tryptophan (1), tyrosine (1) | (1) Peterson, Fred and Domogalla (1925)<br>(2) Vallentyne (1954) |
| Freshwater sediments (peat and gyttja) | α-Alanine (1,3,4), arginine (1,3), aspartic acid (1,4), cystine (3), glutamic acid (1,4), glycine (1), histidine (3), isoleucine (2), leucine (1,2,3), lysine (1,3), serine (1), tyrosine (3), valine (1) | (1) Davidson, Sowden and Atkinson (1951)<br>(2) Robinson (1911a, 1911b)<br>(3) Shabarova (1950)<br>(4) Vallentyne (1954) |
| Terrestrial soil | α-Alanine (1–3, 7–11), β-alanine (1–3, 8), α-aminobutyric acid (2,3), γ-aminobutyric acid (1–3), arginine (1–3,5,7,8), aspartic acid (1–5, 7–11), cystine ? (9), cysteic acid (3), α, ε-diaminopimelic acid (2,3), glutamic acid (1–4, 6–11), glycine (1–4, 7–10), histidine (1–3, 7,8,11), hydroxyproline (2,3,5,8), isoleucine (1,2,6,9), leucine (1,2,4, 6–11), lysine (1–4, 7,8), methionine? (9), methionine sulfoxide (2,3), proline (1–3, 7–9, 11), phenylalanine (1–3, 7–9), serine (1–3, 7–10), threonine (1–4, 7–10), tyrosine (1–4, 9–11), valine (1–4, 6–11) | (1) Adams, Bartholomew and Clark (1954)<br>(2) Bremner (1950a, 1950b)<br>(3) Bremner (1955)<br>(4) Davidson, Sowden and Atkinson (1951)<br>(5) Kivekas (1939)<br>(6) Kojima (1947)<br>(7) Okuda and Hori (1954)<br>(8) Parker, Sowden and Atkinson (1952)<br>(9) Sowden (1955)<br>(10) Stevenson *et al.* (1952)<br>(11) Susuki (1908) |

SESTON. Mazur and Clarke (1942) found the following free amino acids in seston rich in *Gleotrichia echinulata*: tyrosine, tryptophan, cystine, histidine, arginine and lysine. Joyce C. Lewin (1954) has demonstrated that cysteine, methionine and glutathione restore impaired silicon uptake by marine diatoms. In view of the inferred presence of sulphhydryl groups in the diatom cell

membrane, the environmental distribution of sulphur-containing amino acids may be of ecological importance.

WATER. Much remains to be learned about the proteinaceous compounds of dissolved organic matter. The work of Peterson, Fred and Domogalla (1925) was done before the days of amino acid chromatography, and their results (see Table II) need confirmation. It should be noted that table II of their paper is incorrectly titled: the quantitative data for tryptophan, cystine, histidine and tyrosine are actually given as mg. of amino acid-N per m.$^3$ of water, and not as mg. of amino acid per m.$^3$ of water as they state. Vallentyne (1954) failed to identify any of the amino acids listed by Peterson, Fred and Domogalla (1925) as the dominant amino acids in hydrolysates of the dissolved organic matter of lake water. However, Vallentyne's work suffers from the application of insufficient material to the chromatogram. Peterson's group found that the total $\alpha$-amino-N comprised nearly 60% of the total organic-N. Somewhat lower values were recorded by Fogg and Westlake (1955) who have extended this work to seven lakes and two reservoirs in the United Kingdom. The whole question of extracellular algal products has been opened up anew with Fogg's (1952) demonstration that cultured *Anabaena cylindrica* may produce equal amounts of extracellular and intracellular peptide-N. The subject has been reviewed by Fogg (1952) and Fogg and Westlake (1955). The latter have shown that extracellular polypeptide may be ecologically important as a chelating agent, if it is produced under natural conditions.

Bragagnolo (1949) passingly refers to the presence of glutathione in the water of mineral springs. The methods of analysis are not stated.

SEWAGE. Rudolfs and Heinemann (1939) reported the presence of free and combined tyrosine and tryptophan in sewage and digested sludge. (See also Addendum.)

SEDIMENT. Apart from the information listed in Table II little can be said. Gross fractionation of the nitrogen compounds liberated by hydrolysis of lake sediments was carried out by Konshin (1939) and Shabarova (1950). These workers both agree that the monoamino-monocarboxylic acid fraction composes most of the amino acid-N. Shabarova (1950) specifically states that tryptophan is absent from basic hydrolysates.

Free amino acids occur in 10% ethanolic extracts of *Sphagnum* (Black, Cornhill and Woodward, 1955). The following were detected on paper chromatograms: aspartic acid, glutamic acid, glycine, $\alpha$-alanine, serine, threonine, tyrosine, $\alpha$-aminobutyric acid, valine, leucine and/or isoleucine, methionine, arginine, histidine, lysine, proline, asparagine and glutamine. Dried young *Sphagnum* peat on similar extraction yielded only free glutamic acid and $\alpha$-alanine. Tryptophan is stated to be destroyed during humification of *Sphagnum* proteins.

SOIL. The first amino acids to be isolated from soils were histidine and arginine (Schreiner and Shorey, 1910a, 1910b; Schreiner and Lathrop, 1911a, 1911b) and later lysine (Shorey, 1913). Tokuoka and Dyo (1937), using similar

methods (2% NaOH extraction) also reported the occurrence of arginine and histidine. Since these amino acids were recovered from 2% NaOH extracts at room temperature, the inference is that they occurred free in the soil; however, Sallans *et al.* (1937) have questioned this. More gentle extraction with sodium pyrophosphate has failed to reveal the presence of free amino acids in the humic acid fraction of soils (Okuda and Hori, 1954). Bremner (1949, 1950a, 1950b) examined a variety of soils for free amino acids, but failed to detect any. Although Kivekäs (1939) had some evidence of free amino acids in soils (volatile aldehydes produced after reaction with ninhydrin) he felt that the aldehydes were generated by the breakdown of peptide during soil treatment. Using other techniques (analysis of the liquid exuded from soils by pressure) Dadd, Fowden and Pearsall (1953) were able to demonstrate the presence of free amino acids in soil. The total free $\alpha$-amino-N in the exudates of seven samples ranged from 0.4 to 2.5 mg./l. The commonest free amino acids were serine, glycine, aspartic acid and glutamic acid. Less common were leucine and/or isoleucine, threonine and valine. Occasional samples contained $\beta$-alanine, $\gamma$-aminobutyric acid, asparagine and glutamine. There was an inverse relation between pH (3.0 to 6.6) and the concentration of free amino-N.

The possibility of deamination of amino acids by nitrites in acid environments has been investigated by Allison and Doetsch (1951) and Allison, Doetsch and Sterling (1952). These workers concluded that chemical deamination by nitrous acid was unlikely to be of any quantitative importance in soils. Using an atmosphere of NO and a pH of 4.1 only 6% deamination occurred over a period of 3 days. Conditions in natural soils would be much less favourable for the reaction.

Bremner (1950b) has shown that D-amino acids in soil hydrolysates compose 1.7% or less of the total amino acids. This is to be expected in view of the biological origin of these compounds.

COMMENTS. It will be apparent that much remains to be learned about proteinaceous substances in seston, water and sediments. The demonstration of free amino acids in soil water poses a problem for future work, because there should be a rapid uptake of these compounds by microorganisms unless they are in some way protected. Although Peterson, Fred and Domogalla (1925) inferred the presence of free amino acids in the dissolved organic matter of lake water, their methods were indirect, and the data need verification. J. Shapiro (personal communication) reports negative findings for free amino acids in the dissolved organic matter of lakes. Several different microtechniques were used by Shapiro. One important generalization that has come from the study of soil organic-N is the finding that the total $\alpha$-amino-N composes only one-third or slightly more of the total soil organic-N. The $N \times 6.25 =$ crude protein equation can no longer be used.

## PURINES AND PYRIMIDINES

So far as I am aware, purines and pyrimidines have not yet been isolated from either seston or sewage. Studies on other natural sources have either been

suggestive or were, with one exception, carried out 40 years ago and need repeating.

WATER. The only reference to these compounds in water is given by Peterson, Fred and Domogalla (1925) who reported purine-N in their systematic analysis of organic matter dissolved in Lake Mendota water. No specific purines were identified. Hüttel (1941) suggested that the alarm substance of the minnow *Phoxinus laevis* (see Hasler, 1954) behaved like a purine or pterine, but again no specific substance was indicated.

SEDIMENT. Bottomley (1917) isolated and characterized two dinucleotides from peat: a guanine-cystosine dinucleotide and an adenine-uracil dinucleotide. The dinucleotides themselves were not well characterized, but both preparations liberated pentose sugar and orthophosphoric acid on hydrolysis, in addition to the purines and pyrimidines which were adequately identified by crystalline derivatives and colour tests. Shabarova (1950) referred to small amounts of purines in lake mud, but no specific purines were identified.

SOIL. The following have been isolated as crystals or crystalline derivatives from soils: xanthine (Schreiner and Shorey, 1910a, 1910c; Schreiner and Lathrop, 1911a, 1911b; Schreiner and Lathrop, 1912; Lathrop, 1917); hypoxanthine (same references as for xanthine); adenine (Schreiner and Lathrop, 1912; Lathrop, 1917); guanine (Lathrop, 1912; Schreiner and Lathrop, 1912; Wrenshall and Dyer, 1941); and cytosine (Schreiner and Shorey, 1910a, 1910c; Schreiner and Lathrop, 1911a, 1911b; Lathrop, 1917). With the exception of guanine, these purines and pyrimidines were found free in 2% NaOH extracts. Although extraction was conducted at room temperature, it is possible that the purines and pyrimidines were produced by hydrolysis during isolation. On the other hand, guanine has been found only in 2% NaOH extracts of steam heated soils (Schreiner and Lathrop, 1912; Lathrop, 1912) and in soil hydrolysates (Wrenshall and Dyer, 1941). It is noteworthy that Adams, Bartholomew and Clark (1954) failed to detect guanine and adenine on paper chromatograms of soil hydrolysates. The method used was quite sensitive. These workers suggested that nucleic acid-P accounts for less than 5% of the soil organic-P.

## MISCELLANEOUS NITROGEN COMPOUNDS

SESTON. Kapeller-Adler and Vering (1931) found traces of monomethylamine in a 50-g. sample of freshwater seston, but no trimethylamine. Riegel *et al.* (1949b) isolated trimethylamine from *Gonyaulax*-rich marine seston, and identified it by odour and the proportion of Au in the chloroaurate. Choline was found in the same sample, and its identity verified by determining mixed m.p. of the sestonic and authentic picrates and chloroaurates. Riegel *et al.* (1949b) also presented evidence of the occurrence of a betaine-type base in *Gonyaulax*-rich seston.

WATER. Nothing definite seems to be known about the identity of non-amino acid organic-N compounds in the dissolved organic matter of either fresh or salt

water. Braus, Middleton and Walton (1951) obtained data suggestive of the occurrence of pyridine or pyridine-type compounds in water coming from a municipal supply source. Imamura (1952) examined sea water for the presence of phytohormones (auxins) similar to $\beta$-indole acetic acid, but found no evidence of their presence.

SEWAGE. Rudolfs and Chamberlin (1932) reported evidence of indole and skatole in raw sewage. The identifications were based on steam distillation and colorimetric tests on ether extracts of the distillates.

SEDIMENT. Shorey (1913) isolated a substance from a salt marsh deposit by distillation with MgO and subsequent precipitation by potassium ferrocyanide in HCl. The odour and formation of a chloroplatinate indicated the presence of trimethylamine.

SOIL. $\alpha$-Picoline-$\gamma$-carboyxlic acid deserves a special place among this list since it was the first pure crystalline compound isolated from any of the sources under review. It was first isolated from a Hawaiian soil by Shorey (1907) and later from American soils (Schreiner and Shorey, 1908, 1909). Shorey and Walters (1914) isolated a compound called tetracarbonamid from soils, but later work by Wise and Walters (1917) showed that this material was actually cyanuric acid since it had a molecular weight of 130, and not higher as would have been the case for the supposed tetracarbonamid. Ichikawa (1936) also isolated cyanuric acid from soil.

Choline was isolated from soil by Shorey (1913), and characterized by the the m.p. of the chloroplatinate and the % Au in the Au salt. Shorey (1911, 1912) isolated creatinine from soil and characterized it by % N, % Zn in the $ZnCl_2$ salt, and by colour reactions. The method of isolation of creatinine was such as not to convert much creatine to creatinine. Shorey therefore proposed that creatinine occurred as such in soil. The concentration was a few parts per million parts of dry soil. Similar quantities of allantoin were obtained from soil by Shorey (1938). The allantoin was identified by N content, m.p. and chemical reactions.

Because of the possibility that auxins may occur in aquatic sediments, it seems suitable to mention that auxins occur in soil (Parker-Rhodes, 1940; Stewart and Anderson, 1942; Stewart, Keys and Anderson, 1942; Hamence, 1946). The specific identity of these auxins is not known.

## FATS, WAXES, NON-NITROGENOUS ACIDS AND ALCOHOLS

SESTON. Collin, Drummond and Hilditch (1934) isolated cetyl alcohol (m.p., m.p. of phenylurethane derivative, C and H analysis) from the unsaponifiable fraction of marine zooplankton (mostly *Calanus*) oil. They also found an unidentified unsaturated alcohol which gave eicosyl alcohol on reduction by $H_2$ with a palladium catalyst. Lovern (1935) examined marine and freshwater planktonic Crustacea for fatty acids (after saponification). He found that freshwater zooplankton was richest in $C_{16}$ and $C_{18}$ unsaturated fatty acids and marine zooplankton in $C_{20}$ and $C_{22}$ unsaturated fatty acids. According to Mazur and

Clarke (1942), about one-half of the total lipid of seston rich in *Gleotrichia echinulata* is composed of free acids, roughly one-half of these being unsaturated. Clarke and Mazur (1941) report that free palmitic and stearic acids occur in marine seston. Glycerol (after saponification) was identified in marine seston by Clarke and Mazur (1941). Apparently nothing further than this is known about seston.

WATER. Goryunova (1952) reported the occurrence of high molecular weight fatty acids in the dissolved organic matter of Lake Glubokoje, Russia. Braus, Middleton Walton (1951) also obtained data suggestive of the occurrence of high molecular weight fatty acids in water (raw and filtered municipal water). Creac'h (1955) recently reported the occurrence of citric and malic acids in littoral marine water, with concentrations of 0.14 and 0.28 mg./l. respectively. The data, however, are based only on acetone and acetaldehyde production after oxidation with dilute $KMnO_4$. Further substantiation is required.

SEWAGE. Rudolfs and Heinemann (1939) found volatile fatty acids (by distillation) in sewage and sludge. Acetic, propionic and butyric acids were found both in sewage and sludge, but valeric acid (*n*-valeric?) only in fresh solids and not in digested sludge. (See also Addendum.)

SEDIMENT. Because of the probable similarity of waxes isolated from lignites and bituminous coals to those obtained from peat, some workers have extended the methods of wax and resin analysis used on lignites to recent peats. Fatty acids with an odd number of C atoms have been reported to occur in peat waxes (Zaloziecki and Hausmann, 1907; Stadnikov and Sabavin, 1929; Rakovski and Edelstein, 1932; Titow, 1932) as well as in the older lignites. In many cases it is probable that the fatty acid preparations were not pure, but consisted of mixtures of fatty acids with an even number of C atoms (Holde, Bleyberg and Vohrer, 1930; Reilly, Kilbride and Wilson, 1943). The problem of purity is in need of further critical investigation. One must take this into consideration when viewing the results summarized below.

Fatty acids ranging from $C_6$ to $C_{30}$ have been isolated from peat waxes. Stadnikov and Sabavin (1929) obtained fractions resembling caproic ($C_6H_{12}O_2$), heptoic ($C_7H_{14}O_2$) and caprylic ($C_8H_{16}O_2$) acids from saponified peat wax. They concluded (from C and H analysis) that the preparations were not pure, but were mixtures of saturated and unsaturated acids. The $C_6$–$C_8$ acids were calculated to have formed 0.2 to 0.3% of the peat (on a dry weight basis).

Titow (1932) obtained acids of the composition $C_{12}H_{22}O_2$ and $C_{14}H_{26}O_2$ (C and H analysis, eq. wt.) from peat waxes. These acids were thought to have been unsaturated and perhaps partly cyclic as well. Titow (1932) reported the presence of pentacosanoic ($C_{25}H_{50}O_2$) and heptacosanoic ($C_{27}H_{54}O_2$) acids (m.p., C and H analysis, acid No.) in the same material as above. A preparation of the empirical formula $C_{30}H_{60}O_3$ was also isolated. This material melted at 90–91°C., contained 76.76% C and 13.09% H, and was plausibly considered to be an oxy-acid. Rakowski and Edelstein (1932) isolated cerotic ($C_{26}H_{52}O_2$), heptacos-

anoic ($C_{27}H_{54}O_2$) and montanic ($C_{28}H_{56}O_2$) acids from peat waxes. Identifications were based on C and H analysis, m.p. and eq. wt. The heptacosanoic acid may have been a mixture of the $C_{26}$ and $C_{28}$ acids (Rakowski and Edelstein, 1932).

Waxes have been isolated from peat which resemble "montan wax" isolated from older lignites (Thiessen and Johnson, 1930; Johnson and Thiessen, 1934). Other peat waxes (called "mona waxes") appear to have lower melting points than montan wax and differ in other physical properties (Reilly and Emlyn, 1940; Reilly and Wilson, 1940; Cawley and King, 1945). Mona wax liberates cerotic ($C_{26}H_{52}O_2$) and montanic ($C_{28}H_{52}O_2$) acids on saponification (Reilly and Wilson, 1940). The isolated acids were characterized by C and H analysis (m.p., and m.p. of esters). The low melting points (up to 10°C. too low) of the acids were suggestive of impurities (Reilly and Wilson, 1940). Reilly, Kilbride and Wilson (1943) obtained practically pure behenic acid ($C_{22}H_{44}O_2$) from refined "mona wax" derived from Irish peat. The behenic acid was characterized by C and H analysis, m.p. and eq. wt. X-ray data for the isolated behenic acid showed 2 to 5% contamination with arachidic acid ($C_{20}H_{40}O_2$), but only traces of lignoceric acid ($C_{24}H_{48}O_2$) were present.

Although waxes are present in non-peaty sediments, they appear to have been little studied. After saponification of organic solvent extracts of marine sediments, Trask and Wu (1930) obtained evidence of caproic acid ($C_6H_{12}O_2$) (m.p., smell), cerotic acid ($C_{26}H_{52}O_2$), melissic acid ($C_{30}H_{60}O_2$) and possibly montanic acid ($C_{28}H_{56}O_2$) as well. Cerotic acid was also found in organic solvent extracts of lacustrine mud (after saponification). Detailed descriptions of methods, purification procedures and analytical data are not presented.

The alcohol moieties of the sediment waxes have been observed only in a few cases. Zaloziecki and Hausmann (1907) isolated an unidentified alcohol (m.p. 124–130°C., 70.06% C and 11.58% H) from a peat wax (after saponification). Titow (1932) obtained evidence of heptacosanol ($C_{27}H_{56}O$) with the identification based on C and H analysis, m.p. and acetyl No. There was no addition of halogens. Titow (1932) also observed a vaseline-like mixture of alcohols during the same study. Trask and Wu (1930) examined saponified organic solvent extracts of marine and fresh water sediments for higher alcohols, but found only negative evidence.

Fats (glycerides) have apparently not been detected in sediments, nor has the trihydric alcohol, glycerol.

Formic, acetic and butyric acids have been reported to occur in the free state in lake sediments (Kusnetzov, 1934a, 1934b; Kusnetzov and Kusnetzova, 1935; Speranskaja, 1935). Surface sediments differed little in free fatty acid content from immediately sub-surface sediments, except in some cases where acetic acid was concentrated at the surface. Speranskaja (1935) found the following percentages of free acids in the dry organic matter of sediments from four lakes: formic acid, 0.00 to 0.36%; acetic acid, 0.04 to 2.30%; and butyric acid, 0.09 to 0.73%.

SOIL. Purified waxes and fats have not been isolated from soils. Schreiner and Shorey (1910a, 1911b) have, however, detected glycerol (acrolein test) after saponification of soil lipids. The acids liberated by saponification were not unequivocally identified.

Considerable interest centers around the occurrence of inositol (inosite) in soils, since it is complexed with phosphoric acid. Shorey (1913) referred to evidence of inositol in soil extracts, but he did not succeed in separating the pure compound. This has since been achieved by Sallans *et al.* (1937) (mixed m.p., m.p. of hexaacetate), Yoshida (1940) (mixed m.p., C and H analysis), Dyer *et al.* (1940) and Bower (1945). There is some question as to the nature of the soil inositol-P compounds. Yoshida (1940) suggested that phytin (inositol hexaphosphate) was not the only inositol-P compound in soil. Bower (1945) later reported that phytin accounted for 33% of the soil organic-P and other inositol-phosphates only 12%. Norgaard-Pedersen (1953) found that 46% of the soil organic-P occurred as phytin. The purity of these phytin preparations has been questioned by Smith (1952) who separated inositol-phosphates on anion exchange columns. Inositol-phosphates have not been reported from aquatic sediments, apparently because no one has looked for them.

The acids (seemingly free) which have been isolated from soils are listed in Table III. A summary of the isolation procedures used for free acids and other soil constituents is given by Schreiner and Shorey (1911a).

TABLE III.—Free, non-nitrogenous acids in soils.

| Acid | Characterization | References |
|---|---|---|
| Acetic acid | (Mixed m.p. of *p*-phenylphenacyl acetate) | Osugi and Aoki (1936)<br>Sallans *et al.* (1937) |
| Acrylic acid | (Bromination gives dibromopropionic acid) | Shorey (1913) |
| Benzoic acid | (M.p.; dinitro derivative) | Shorey (1914) |
| 3, 5-cresotic acid (*m*-oxytoluic acid) | (M.p.; C and H analysis; reactions) | Shorey (1914( |
| α-Crotonic acid | (Mixed m.p.; neutralization equivalent) | Walters and Wise (1916) |
| Formic acid | (Reduction of $HgCl_2$) | Osugi and Aoki (1936)<br>Sallans *et al.* (1937) |
| α-Hydroxystearic acid | (M.p.; C and H analysis; Ag in Ag salt) | Schreiner and Shorey (1910a' 1910d)<br>Schreiner and Lathrop (1911a) |
| 8,9-Dihydroxy-stearic acid | (C and H analysis; Ag in Ag salt; mixed m.p.) | Schreiner and Shorey (1908b, 1909)<br>Schreiner and Lathrop (1911a, 1911b, 1911c) |
| Lignoceric acid | (M.p.; C and H analysis) | Schreiner and Shorey (1910a, 1910d)<br>Schreiner and Lathrop (1911a)<br>Tokuoka and Dyo (1937) |
| Oxalic acid | (M.p.; m.p. of paratoluide) | Schreiner (1913)<br>Osugi and Aoki (1936) |
| Saccharic acid | (Ag in Ag salt; K acid salt) | Shorey (1913) |
| Succinic acid | (M.p.; m.p. of paratoluide) | Shorey (1913) |

## ALDEHYDES

SOIL. Aldehydes are known only from soils. Salicylic aldehyde was obtained by Shorey (1913) and characterized by aldehyde reactions as well as the mixed m.p. of the phenylhydrazones from the soil aldehyde and authentic aldehyde. Shorey (1913) also isolated trithiobenzaldehyde from soil. It was characterized by m.p. determination and the formation of stilbene on heating with Cu. Vanillin is to be expected in soils since it is part of the structure of lignin. However, it has only been isolated by Shorey (1914). It was characterized by m.p. determination plus chemical reactions. Methylglyoxal (2-ketopropional) was steam distilled from soil by Enders and Sigurdsson (1942). It was identified by the formation of the 2,4-dinitrophenylosazone which exhibited no m.p. depression when mixed with the authentic osazone.

## LIGNINS

The complexities of lignin chemistry are well known. Lignins are included here not because they are chemically well understood substances, but because they make up such a large part of the organic matter of sediments. Vanillin is the only known lignin constituent which has been isolated from any of the sources under review (Shorey, 1914). The usual method for the determination of lignins in sediments and soils is to determine the weight of ash-free residue left after hydrolysis with cold concentrated and then hot dilute $H_2SO_4$. Since lignins do not contain N and the residues usually do, it is customary to subtract 6.25 times the N content to get the weight of lignin. Lignin values are very suspect (Waksman and Stevens, 1928) since the residues may include other insoluble substances which are resistant to acid hydrolysis. Several workers (Steiner and Meloche, 1935; Sowden and Atkinson, 1949; and others) have questioned whether the lignin fractions from soils and aquatic sediments are really similar to wood and straw lignin preparations. Adequate criteria for identity are lacking. Another complicating factor is that some of the soil and sediment lignin fractions are soluble in the wash water and pass through the filter paper (Waksman and Hutchings, 1935; Sowden and Atkinson, 1949). Furthermore, Steiner and Meloche (1935) demonstrated that the percentage of methoxyl in lignins isolated from different lake sediments was quite variable, and generally lower than that of wood or straw lignin.

The importance of knowing more about lignin fractions of sediments and soils is that they compose about one-third of the organic matter therein (Steiner and Meloche, 1935; Speranskaja, 1935; Kusnetzov, Speranskaja and Konshin, 1939; Hutchinson and Wollack, 1940; Twenhofel, Carter and McKelvey, 1942; Kleerekoper and Grenier, 1952). The resistance of lignins to bacterial and chemical degradation is well known. This leads to their accumulation in the sediments. Lignin, as such, is only slowly decomposed by bacteria and fungi (Waksman and Hutchings, 1936). ZoBell and Stadler (1941) found that lignin in ligno-cellulose preparations was more readily attacked by lignoclastic bacteria than was lignin alone. Waksman and Cordon (1938) found that the presence

of about 8% lignin in ligno-cellulose preparations retarded the bacterial decomposition of the cellulose by about 50%.

Waksman, Carey and Reuszer (1933) reported the occurrence of 7.8% "lignin" in marine zooplankton, but suggested that this value probably represented a polyuronide resistant to hydrolysis rather than lignin. Steiner and Meloche (1935) similarly found 10 to 20% "lignin" in freshwater net and nannoplankton, but again it is quite uncertain that such residues actually are lignins.

Gottlieb and Hendricks (1945) unsuccessfully attempted to isolate known lignin constituents from soils.

Post-glacial lake sediment cores have been analysed for lignins by Ohle (1933), Hutchinson and Wollack (1940) and Twenhofel, Carter and McKelvey (1942). Lignins were found at all depths. There was no marked enrichment of lignins in the organic matter of the deeper deposits. Ohle (1933) interpreted the high methoxyl : lignin ratios at one level in a core from Kleine Ukleisee as indicative of a sediment rich in hydrophyte remains (rather than terrestrial plant remains).

## CHLOROPHYLLS AND RELATED COMPOUNDS

Ever since Harvey's (1934) development of the pigment extraction method for the quantitative assay of phytoplankton populations, a considerable interest has been taken in seston chlorophyll. The most remarkable thing is that no one has isolated in pure form from seston any of the separate chlorophylls known to occur in planktonic algae.

SESTON. The methods used for the determination of chlorophyll have been quite diverse. Harvey (1934) visually compared the colour of acetone extracts to a series of artificial colour standards. Riley (1938) used a similar procedure, but after saponification. Graham (1943) measured chlorophyll by the density of acetone extracts at a wave-length of 668 m$\mu$. Kalle (1951) utilized the property of fluorescence to measure the chlorophyll content of seston. Richards and Thompson (1952) calculated the proportions of chlorophylls *a*, *b* and *c* in marine seston from measurements of light absorption at three different wave-lengths in the red part of the spectrum. This method involves the assumption that chlorophylls *a*, *b* and *c* are the only compounds in acetone extracts of seston which absorb light at these wave-lengths. In many of these methods the amounts of chlorophyll given may be in error because of the use of improper calibration factors. This is particularly true where commercial chlorophyll standards have been used (Manning and Juday, 1941; Atkins and Jenkins, 1953).

It has not been proved that all the chlorophyll as measured is photosynthetically active. Part of the seston is composed of dead matter. Kozminski (1938) refers to photosynthetically inactive chlorophyll in the seston of deep water, but it is not clear whether he is speaking of chlorophyll in healthy cells in the dark depths of lakes or chlorophyll in dead cells. In some of the Wisconsin lakes studied by Kozminski the chlorophyll was found to comprise a higher percentage of the organic mater of deep water seston than of surface water seston. In many of

these cases the deep water was below the compensation depth. The only study of the fate of chlorophyll in decomposing plankton is that of Skopintsev and Bruk (1940). They found that 82% of the chlorophyll in fresh plankton had disappeared after 53 days' decomposition at 16° C. The corresponding value for decomposition at 6° C. was 52%.

In spite of the wide variation of chlorophyll content with species and growth conditions, the pigment method appears to have validity as a rapid method of estimating phytoplankton populations, but only when series of samples are compared to each other (Tucker, 1949). Margalef (1954), on the other hand, believes that pigment concentrations are not a sound measure of standing crops.

The chlorophyll content of seston is stated to be a good measure of photosynthetic capacity by Manning and Juday (1941) and Gessner (1943), but the limited data given by Manning and Juday are selective, and their complete data do not appear to lead so easily to their conclusion. Ryther (1956) found a direct relation between the amount of photosynthesis and the amount of chlorophyll *a* for several species of algae. He has suggested that primary production may be computed from a knowledge of chlorophyll and light energy. At the present time the data appear to be too limited, and depend on too many assumptions, to warrant a general application of this principle. Rodhe, Vollenweider and Nauwerck (1956) report that seston chlorophyll and $C^{14}$ production rate are proportional during the spring diatom bloom, but not during the summer when the total plankton population fluctuates to a smaller extent.

Algae grown in the laboratory are known to change their colour when the wave-length of light used for culture is varied. Dutton and Juday (1944) chromatographed seston extracts from a series of depths in several lakes, but obtained no evidence that the proportions of different pigments were in any way related to the variation of light spectra with depth.

WATER AND SEWAGE. Chlorophyll compounds and their derivatives have not been reported to occur in dissolved organic matter or sewage.

SEDIMENT. The chlorophylls known from fresh plant tissues, although looked for, have not been found in either marine or freshwater sediments (Fox and Anderson, 1941; Fox, Updegraff and Novelli, 1944; Vallentyne, 1955). There do occur, however, a variety of green lipoidal pigments in sediments. These have absorption spectra similar to those of the known plant chlorophylls. Vallentyne (1955) has proposed collectively calling these sedimentary chlorophyll, but as this might imply that the compounds actually are of the chlorophyll structure, it is perhaps better to call them sedimentary chlorophyll degradation products (SCDP).

Evidence of SCDP in freshwater and marine sediments is presented by Baudisch and von Euler (1934), Jastrebova (1938), Klenova and Jastrebova (1938), Torstensson, Eriksson and Wiklander (1939), Wells and Erickson (1940) and Titov (1950). None of these workers resorted to spectrometry or chromatography. Absorption maxima of crude sediment extracts are given by Lubimenko and Rauser-Cernooussova (1930) for freshwater sediments and Brongersma-

Sanders (1951, see appendix by W. G. Aldershoff) and Rauser-Cernooussova (1930) for marine sediments.

There can be little doubt that the green lipoidal substances of sediments were formed from plant chlorophylls. Although none of the decomposition products has been identified, partial purifications have been achieved by chromatography. Beatty (1941) separated a chlorophyll-like fraction from extracts of cave sediments. The absorption bands were stated to be similar to "chlorophyll". Koltz (see Phinney, 1946) obtained chromatographic fractions similar to chlorophylls *a* and *b* (but with different absorption maxima) from sapropel estimated to be 15,000 to 26,000 years old. The age was probably overestimated by a factor of 2. Titov (1950) refers to the formation of chlorophyllides in lake sediments. He found a pigment not extractable with benzene, but extractable with ethanol. This pigment was stated to be related to chlorophyll *b*. Andersen and Gundersen (1955) found five different green spots on paper chromatograms of extracts of an interglacial gyttja. The two main absorption maxima for these pigments were between 410 and 420 m$\mu$ and 670 and 680 m$\mu$ (acetone as the solvent). Vallentyne (1955) found three green fractions on paper chromatography of sediment extracts, all with absorption maxima at 412 and 667 m$\mu$. More recent work by Brown (unpublished) has shown that these three green fractions were mixtures; he has isolated four different green pigments with the main absorption maxima (in acetone) at the following wave-lengths: 411, 670; 425, 660; 440, 662; and 464, 656 m$\mu$. There was also evidence of other pigments with chlorophyll-like spectra, but these were not studied in detail.

Working with marine sediments, Fox and Anderson (1941) described the isolation of three SCDP fractions. One of these was soluble in petroleum ether and could be separated into two chromatographic zones. The second was insoluble in petroleum ether, but soluble in acetone. The third was insoluble in petroleum ether with or without acetone, but was soluble in aqueous acetone.

The processes which give rise to chlorophyll degradation products are unknown. It is not even certain if phytyl and Mg are present in the degraded molecules. Trask and Wu (1930), however, noted that Mg was present in the ash of a SCDP fraction from marine mud. Although breakdown of chlorophylls is known to occur in animal digestive tracts (Fox, Crane and McConnaughy, 1948, and references therein) such processes must be quantitatively inadequate to explain the degradation products of sediments. Chemical, photochemical, and enzymatic processes must all be involved.

The preservation of SCDP for thousands of years seems remarkable, but one must remember that the sediment is devoid of light and oxygen, factors which tend to destroy chlorophylls. Jastrebova (1938) reported a sharp decline in the amounts of SCDP from the surface to a depth of 30 cm. in marine sediments, but on the other hand Fox (1944) has found SCDP in marine sediments estimated to be 4,000 years old. Working with lake sediments, Vallentyne (1955) found that some lake deposits had the greatest amount of SCDP per unit ignitable matter in the oldest (9,000 to 11,000 years) organic sediments. The oldest known sample containing SCDP is the 100,000-year-old gyttja studied by Andersen and

Gundersen (1955). The use of SCDP concentrations as a semi-quantitative measure of chlorophyll-bearing plant matter deposited during the history of a lake has been advocated, with caution, by Vallentyne (1955).

That reducing conditions favour the stability of chlorophylls in the laboratory is well known. Klenova and Jastrebova (1938) have accordingly suggested that it may be possible to determine past changes in the gas regimens of water bodies by analysing sediment cores for SCDP. In this connection Brongersma-Sanders (1951) pointed out that chlorophylls should be best preserved in sapropels (sediments deposited under anaerobic conditions). The obvious implication to limnology is that it may be possible to imply the time of onset of meromixis in meromictic lakes.

SOILS. Kamoshita (1942) reported reddish fluorescence of acetone extracts of soils. He attributed the fluorescence to the presence of "chlorophylls".

REMARKS. More exact identification of chlorophylls and related compounds is necessary before much meaning can be attached to the data outlined above. Studies of chlorophyll degradation during plankton decomposition merit special attention. If one could separate and identify the degradation products of chlorophylls *a*, *b* and *c* in sediments, a refined paleobiology might be developed. True porphyrins have never been isolated from recent sediments, although they are known from older sedimentary rocks.

## CAROTENOIDS

SESTON. Of the great variety of carotenoids known to occur in planktonic algae, only a few have been identified in seston. According to Gillam, El Ridi and Wimpenny (1939) and Fox (1937) hypophasic carotenoids predominate over the epiphasic in marine seston.

Heilbron and Lythgoe (1936) isolated the following carotenoids from a collection of seston rich in *Oscillatoria rubescens*: $\beta$-carotene (m.p., absorption spectrum); myxoxanthin (m.p., absorption spectrum); myxoxanthophyll (m.p., absorption spectrum, C and H analysis) and lutein (m.p., absorption spectrum, C and H analysis). From a sample of pond seston rich in *Aphanizomenon flos-aquae*, Tischer (1938) obtained aphanin (=myxoxanthin=echinenone; m.p., mol. wt., C and H analysis), flavacin (m.p., absorption spectrum), $\beta$-carotene (m.p., absorption spectrum, C and H analysis) and aphanizophyll (=myxoxanthophyll?; m.p., mol. wt., C and H analysis). Kylin (1927) obtained peridinin (=sulcatoxanthin?) from pond seston rich in Peridineae. Pinckard *et al.* (1953) also report peridinin (crystals, absorption spectrum) together with $\beta$-carotene in marine seston rich in the peridinian *Prorocentrum micans*. The nature of the haematochromes which Kylin (1927) isolated from pond seston rich in *Euglena* is not clear to me.

The carotenoid astaxanthin (converted to astacene during most isolations) is found almost exclusively in the animal kingdom. Lederer (1938a) obtained astacene (120 mg. of crystals isolated) together with small amounts of $\beta$-carotene

from *Calanus*. The presence of astacene (more accurately astaxanthin) as the only carotenoid in euphausiids has been shown by Drummond and MacWalter (1935), and Fisher, Kon and Thompson (1952, 1954, 1955). Kon (1954) has reviewed work done on the isolation of carotenoids from marine zooplankton, especially in relation to vitamin A production (see also the section on vitamins).

Carotenoids are susceptible to photochemical oxidation. Gross changes may be expected to occur not only during isolation, but also in the natural environment. Baldi (1941), for example, noted great variations in the colour of *Glenodinium* in Lago di Tovelli. He showed that when the red coloured algae were brought to the laboratory and kept in the dark they became colourless; but on exposure to light, again turned red. The colour changes were thought to be associated with carotene-rich oil droplets in the cells.

WATER. Lucas (1947) refers more than once to the importance of carotenoids free in water, but does not give the source of his information. Johnston (1955) has reported that carotenoid-like coloured matter is present dissolved in sea water. No more than minute amounts of free carotenoids could occur in water, due to their low solubility.

SEWAGE. Carotenoids occur in sewage (Rudolfs and Heinemann, 1939) but no pure compounds have been isolated.

SEDIMENT. Although studies of sedimentary carotenoids are still in an early stage, a considerable amount of work has been done. Unlike the sedimentary chlorophyll degradation products, most of the carotenoids appear to be the unchanged constituents of the organisms that produced them. The presence of carotenoids in lake sediments was first indicated by Trask and Wu (1930). Carotenes (mostly $\beta$-carotene) and xanthophylls were later found by Baudisch and von Euler (1934) and Baudisch (1938) in Swedish gyttja. Johnson and Thiessen (1934) passingly refer to both epiphasic and hypophasic carotenoids (carotenes and xanthophylls, respectively) in peat. Klimov and Kazakov (1937) made a study of the carotenes in lake and marsh sediments, finding the latter source richer than the former. Muraveisky and Chertok (1938) studied the amounts of carotenes and xanthophylls in lake sediments. They found the xanthophylls to predominate in most samples. Occasional lake sediment samples were lacking in carotenoids. Lederer (1938b) isolated 1 mg. of crystalline carotene from an extract of Lake Biserovo sediment, together with a small amount of myxoxanthin (=echinenone), two unidentified crystalline xanthophylls and eleven other hypophasic carotenoids. Karrer and Koenig (1940) studied an extract of pink sediment from Lake Nakuru, Kenya Colony. Since the extract had a spectrum exactly superposable on that of rhodoviolascin these workers concluded that the main carotenoid was rhodoviolascin, and that it had originated from purple bacteria in the sediment. Beatty (1941) reported $\beta$-carotene and other carotenoids to be present in cave sediments, and suggested the possible nutritional value of sedimentary carotenoids to animals living in a dark environment. Titov (1950) found carotenoids in concentrations up to 3 mg./100 g. of

dried lake sediment. $\beta$-Carotene was isolated from lake and medicinal muds by Savinov, Mikhailovnina and Shapiro (1950). The isolated compound was shown to be chromatographically inseparable from an authentic specimen of $\beta$-carotene. Total unsaponifiable pigments occurred in concentrations of 0.9 to 5.7 mg./100 g. wet weight. Vallentyne (1954, 1956) found carotenoids in lake sediments estimated to be 11,000 years old. From a 20,000-year-old sediment sample from Searles Lake, California, Vallentyne (1957) isolated the following: $\alpha$-carotene, $\beta$-carotene, neo-$\beta$-carotene B, and neo-$\beta$-carotene U (identities proved by co-chromatography and superposable absorption spectra with the authentic compounds). The *cis*-isomers (neo-B and neo-U) were shown to be mostly (if not entirely) isolation artifacts. Echinenone was provisionally identified. The oldest deposit from which carotenoids have been isolated is from the Rodebaek I horizon (interglacial) in Denmark, estimated to be 100,000 years old. From samples of this deposit, Andersen and Gundersen (1955) separated by paper chromatography four yellow carotenoids (one of which was impure $\beta$-carotene) and two red zones. One of the red zones had a carotenoid-type spectrum, but the identity of the other was uncertain. Züllig (1955, 1956) has developed a method for the determination of xanthophylls in fresh sediments; however, since no chromatography was used, the xanthophyll values may be affected by the presence or absence of SCDP.

The carotenoids of marine sediments have been extensively studied by D. L. Fox and his associates. Fox (1937) first drew attention to the presence of carotenoids in marine sediments, identifying by chromatography and spectra $\alpha$- and $\beta$-carotenes. Fox and Anderson (1941) verified the presence of these two carotenes and also reported the occurrence of fractions similar to rhodopurpurin, torulene and astacene. Approximately 6 mg. total carotenoids per 100 g. dry sediment was found. The stability of carotenoids in marine sediments was indicated by their presence in deposits estimated to be 7,000 years old. Further and more extensive analyses of sedimentary carotenoids were made by Fox (1944) and Fox, Updegraff and Novelli (1944). They tentatively identified the following carotenoids in extracts of marine sediments (using chromatography and spectra): $\alpha$-carotene, $\beta$-carotene, rhodopurpurin, flavorhodin, torulene, fucoxanthin, petaloxanthin, zeaxanthin (or diatoxanthin), sulcatoxanthin (= peridinin?) antheroxanthin, glycymerin, leprotene and astacene(?). Other carotenoids were found, but not identified.

Sedimentary carotenoids are not necessarily as old as the deposit which contains them. The possibility of post-depositional synthesis by microorganisms in the sediment has been suggested by Fox, Updegraff and Novelli (1944). It is furthermore possible that calcareous deposits may selectively adsorb hypophasic carotenoids (Baudisch and von Euler, 1934; Beatty, 1941; Titov, 1950).

The degradation of carotenoids in sediments probably occurs through the agency of microorganisms in the sediment (Fox, 1948). This biological degradation is likely to be effective only in near-surface sediments where living microorganisms are concentrated. Destruction of xanthophylls, but not carotenes,

occurs in the gut of the marine annelid *Thoracophelia* (Fox, Crane and McConnaughy, 1948). Fox and Oppenheimer (1954) found that zeaxanthin was unaffected by pressures up to 730 atmospheres in the presence of $H_2$ or $H_2S$, with or without the addition of marine mud. Similar pressures in a $CO_2$ atmosphere caused some destruction of zeaxanthin in the presence of marine mud, presumably due to the acidity developed. Fox and Oppenheimer concluded that chemical reduction of xanthophylls by high pressures of reducing gases is unlikely to occur in nature.

REMARKS. The presence of carotenoids in sediments, as well as their stability therein, have been well verified. Only in a few cases, however, have pure crystalline compounds been isolated or the single chromatographic zones run on mixed chromatograms with authentic specimens. It should also be noted that some workers who list absorption maxima for carotenoids fail to mention the solvent used. In such cases the published information is of little value because of the pronounced shifts of absorption maxima with different solvents.

## STERIDS AND OTHER NON-CAROTENOID HYDROCARBONS

SESTON. Hydrocarbons (paraffinic, naphthenic and aromatic) occur in marine seston in amounts up to two parts per thousand (Smith, 1954). For the most part their molecular nature is unknown. Collin, Drummond and Hilditch (1934) isolated a hydrocarbon resembling squalene ($C_{30}H_{50}$) from marine zooplankton oil, but it was not specifically identified. They also referred to the presence of cholesterol(?) in a digitonin precipitate from the same source. Belloc, Fabre and Simonnet (1930) refer to "biologically active" sterols in seston, but only in summary. Clarke and Mazur (1941) obtained a hydrocarbon fraction from marine seston which agreed with the composition of hentriacontane ($C_{31}H_{64}$) both in C and H analysis and mol. wt. determination. The m.p., however, was 9° C. too low.

WATER. Estrogenic substances are said to occur in mineral waters (Bragagnolo 1949) to the extent of 20 mouse units per litre of water.

SEWAGE. *p*-Cymene has been reported to occur in gases emanating from "municipal refuse" (Roberti, Pera and Simonetti, 1940). Sterols, though doubtless present in sewage, have apparently not been detected therein.

SEDIMENT. Hydrocarbons are present in fresh water and marine sediments in concentrations up to several hundred p.p.m. of dry sediment (Smith, 1954; Swain and Prokopovich, 1954; Swain, 1955; Judson and Murray, 1956; Ginsburg-Karagitscheva and Rodionova, 1935). Paraffinic, naphthenic and aromatic hydrocarbons are all present (Smith, 1954). Trask and Wu (1930) had suggestive evidence of triacontane ($C_{30}H_{62}$) in shallow marine mud. Titow (1932) obtained the following from peat bitumens: pentatriacontane ($C_{35}H_{72}$) and tritriacontane ($C_{33}H_{68}$). These hydrocarbons were isolated as crystals and characterized by m.p., C and H analysis, mol. wt., and negative addition of halogens.

A number of investigators have reported the presence of estrogenic substances in medicinal muds (Kilian, 1937; Rainer and Vladutiv, 1938; Krastins, 1939; Krsnik, Tomić, and Supek, 1944; Bragagnolo, 1949). The specific compounds are unknown, but the amounts range from 15 up to 600 mouse units per kg. of dry sediment.

Trask and Wu (1930) obtained evidence from the presence of "phytosterol" and "cholesterol" in both freshwater and marine muds. The identifications were based on digitonin precipitates and formation of acetates. Montignie (1938) studied unresolved mixtures of plant and animal sterols isolated from peat and lignites. Cosmovici and Atanasiu (1936) isolated a mixture of sterols from sediments formed from decomposing *Cladophora*. Inhabitants of the Black Sea region are stated to obtain some degree of cure for rickets by coating themselves with the mud, then bathing in the sun. The authors believe that irradiated ergosterol may be absorbed through the skin by this procedure. Black, Cornhill, and Woodward (1955) obtained a sterol fraction from *Sphagnum* which corresponded to $\beta$-sitosterol (m.p. of derivatives). Fox and Oppenheimer (1954) found that cholesterol alone, or mixed with marine mud, was not chemically reduced by 730 atmospheres pressure of $H_2$, $H_2S$, or $CO_2$. They suggested that sterols were more likely to be reduced in marine sediments by microorganisms rather than by chemical reactions.

SOIL. Hentriacontane ($C_{31}H_{64}$) was isolated from soils by Schreiner and Shorey (1910a, 1911c) and Schreiner and Lathrop (1911a, 1911b). It was identified by m.p., C and H analysis and general resistance to chemical reactions. There was no m.p. depression when mixed with the authentic compound (Schreiner and Shorey, 1911d). Kern (1947) obtained the polycyclic aromatic hydrocarbon chrysene from soil (mixed m.p., ultraviolet spectrum). Cooper and Lindsey (1953) believe that the chrysene may have originated by the settling of hydrocarbons from polluted air. Schreiner and Shorey (1910a, 1911e) and Schreiner and Lathrop (1911a, 1911b) obtained "phytosterol" from saponified soil extracts. It was characterized only by general properties, m.p. and colour reactions. Schreiner and Shorey (1909) obtained another crystalline sterol from soil (without saponification) which they named agrosterol. Its identity is unknown, but it was probably a mixture (personal communication from Werner Bergmann).

## VITAMINS

It is convenient to discuss each of the vitamins separately, rather than under the headings of environment. When speaking of vitamins as being present in a particular source, one should realize that nearly all the data are obtained by biological assay. In many cases the assay organisms respond to more than one particular form of the vitamin. In other cases the organism may be able to synthesize the vitamin from some component parts. The biological activity of different substances used by the organism to overcome a particular vitamin need may vary. It must be stressed therefore that some of the data referred to below may be both quantitatively and qualitatively in error.

VITAMIN A. With the exception of McCarrison's work (1923) showing the presence of vitamin A-active substances in soil, only seston is known to contain vitamin A. Drummond and Gunther (1930, 1934) reported that phytoplankton collections were vitamin A-active to rats, but zooplankton collections possessed little or no activity. Gillam, El Ridi and Wimpenny (1939) found evidence of the presence of vitamin A in marine seston (ultraviolet peak at 328 m$\mu$ in ethanol). This was apparently the first demonstration that vitamin A itself (and not in the form of carotenoid precursors) was present in seston. It is notable that Gillam *et al.* reported that one diatom-rich sample did not contain vitamin A. Lederer (1938a) examined *Calanus* for vitamin A, but found only negative evidence. Lane (1950) reported that marine zooplankton oil was thirty times as vitamin A-active to the fish *Limanda ferruginea* as was predicted from the $\beta$-carotene content of the oil. The oil was chromatographed on a column of $CaCO_3$–celite. The vitamin A-active fraction passed through the column and was observed to have an absorption peak at 310 m$\mu$ but no 325 peak as would have been the case for vitamin A.

The vitamin A content of euphausiids (krill) has been studied by Fisher, Kon and Thompson (1953, 1954, 1955). The vitamin A which occurs in krill is almost completely limited to the eye. It occurs there mostly in esterified form. Identification was by chromatography and absorption spectra. Fisher *et al.* (1955) reported that eye extracts of the euphausiid *Meganyctiphanes norvegica* contained a *cis*-isomer of vitamin A in addition to vitamin A itself. It is not clear that the *cis*-isomer was not produced during isolation. The fact that *cis*-isomer showed an ultraviolet absorption peak at 311 m$\mu$ suggests that Lane's (1950) factor from zooplankton oil may have been something similar. Kon (1954) has reviewed his work on the isolation of vitamin A and carotenoids from krill.

Natural sources of some carotenoid precursors to vitamin A are mentioned under the heading of carotenoids.

THIAMIN (VITAMIN $B_1$). Hutchinson (1943) found the concentration of thiamin in one sample of lake seston to be 35 mg./kg. dry weight. Hutchinson also demonstrated that 7 to 39% of the thiamin in unfiltered lake water (averaging 0.2 mg. thiamin per m.$^3$) passed through a membrane filter, and was therefore part of the dissolved organic matter. This may be ecologically important since some auxotrophic algae need this vitamin (Provasoli and Pintner, 1953). Hutchinson (1943) found lesser amounts of thiamin in mud than in seston: 2.3 and 3.1 mg./kg. dry weight of mud for two samples analysed. These values corresponded to about 10 mg./kg. ignitable matter of the mud. Ridyard (1946) noted that thiamin is adsorbed by sand. Ecologically, this is interesting because sand is a relatively ineffective adsorbent as compared to clay for most charged compounds. Vitamin $B_1$ has been detected in activated sludge (Kocher and Corti, 1952), and with depth-decreasing concentrations in soil (Lilly and Leonian, 1939; Schopfer, 1945; Roulet, 1948; Roulet and Schopfer, 1950).

RIBOFLAVIN (VITAMIN $B_2$). Only soils (Carpenter, 1943; Schmidt and Starkey, 1951) and activated sludge (Kocher and Corti, 1951) are known to contain

riboflavin. The concentrations in activated sludge ranged from traces up to 7 mg./kg. dry weight.

NIACIN (NICOTINIC ACID, VITAMIN $B_6$). Hutchinson and Setlow (1946) found 33 mg./kg. of niacin in the organic matter of one sample of lake seston. In the lakes studied the dissolved niacin (0.15–0.89 mg./$m.^3$) occurred in concentrations approximately equal to the sestonic (unit volume of water). Activated sludge contains niacin in concentrations of 100 mg./kg. dry weight (Kocher and Corti, 1951). Roulet and Schopfer (1950) report that niacin occurs in soil.

VITAMINS $B_{12}$. This set of vitamins may prove to be of considerable importance in biochemical ecology. The majority of auxotrophic algae require vitamin $B_{12}$ factors in at least one form (Provasoli and Pintner, 1953; Droop, 1954; Sweeney, 1954; R. A. Lewin, 1954). It is usual in the assay of the vitamins $B_{12}$ to autoclave the sample before analysis in order to liberate the vitamins. Assay is complicated by the occurrence of several chromatographically distinct factors, each of which shows vitamin $B_{12}$ activity to *Escherichia coli* mutants. Rabek *et al.* (1956), for example, summarized evidence to show the occurrence of eleven vitamin $B_{12}$-active factors in sewage sludge. Unless otherwise noted, the concentrations of vitamins $B_{12}$ are expressed in terms of the weight of cyanocobalamin. Not all $B_{12}$ factors are as vitamin-active as cyanocobalamin, so the total weight of $B_{12}$ substances may be underestimated by the assay method.

Ericson and Lewis (1953) examined marine seston for vitamins $B_{12}$, but found none (less than 1 m$\mu$g./g. dry weight). On the other hand, Burkholder and Burkholder (1956b) report 2.5–17.5 m$\mu$g. vitamins $B_{12}$ in the suspended matter contained in one litre of estuarine water. The amounts were shown to depend on the method of extraction, being increased when $Na_2SO_3$ was added to the extractant. Burkholder and Burkholder (1956a) found vitamins $B_{12}$ ($Na_2SO_3$ treatment) in river waters in concentrations up to 6.4 $\mu$g./g. of dry sestonic solids. Concentrations up to 73 $\mu$g./g. (no $Na_2SO_3$) were found in salt marsh sediments. Robbins, Hervey and Stebbins (1950) found that the concentrations of vitamins $B_{12}$ in pond water (dissolved) ranged from 0.1 to 1.0 m$\mu$g./l. of water. From the little that is known, sea water appears to contain 5 to 10 m$\mu$g./l. of vitamins $B_{12}$ (Droop, 1954, 1955; R. A. Lewin, 1954). Vitamins $B_{12}$ also occur in activated sludges, the concentrations ranging from 1 to 10 mg./kg. dry weight (Hoover, Jasewicz and Porges, 1951; Kocher and Corti, 1951; Hoover *et al.*, 1952; Whitmarsh, Albans and Wright, 1955). The vitamin $B_{12}$ activity is almost quantitatively associated with the sludge particles (Sjöstrom, Neujahr and Lundin, 1954). The vitamin $B_{12}$ factors of sewage sludge have been chromatographically separated by Friedrich and Berhauer (1953), Sjöstrom, Neujahr and Lundin (1954), Neujahr (1955a, 1955b) and Rabek *et al.* (1956). The presence of eleven separate factors is indicated.

Hashimoto and Sato (1954) mention that pond mud is very rich in vitamins $B_{12}$. Vitamins $B_{12}$ have been detected in soil extracts (Robbins, Hervey and Stebbins 1950).

ASCORBIC ACID (VITAMIN C). Beneden (1949) reported the presence of vitamin C in seston. Wangersky (1952) has identified dehydroascorbic acid (crystals, spectrum) in the dissolved organic matter of sea water.

VITAMINS D. Drummond and Gunther (1930, 1934), Johnson and Levring (1947) and Copping (1934) found that small amounts of vitamin D-active substances were present in marine zooplankton, but not in marine phytoplankton. Johnson and Levring (1947) state that marine phytoplankton contains provitamins D.

BIOTIN (VITAMIN H). Biotin occurs in lake seston and lake water in quantities not exactly determined, but of the order of magnitude of 1 mμg./l. of water (Hutchinson, 1943; Hutchinson and Setlow, 1946). Roulet and Schopfer (1950) found biotin in soil, the quantities decreasing with depth. These workers also state that *Sphagnum* peat, diatom-rich plankton and forest humus are richer sources of biotin than cultivated or pasture soils.

OTHER VITAMINS AND VITAMIN-LIKE SUBSTANCES. Ericson (1953) obtained preliminary evidence of substances related to folic and folinic acid in marine seston. Folic-acid-like substances have been reported to occur in sewage sludge in concentrations a little over 1 mg./kg. dry sludge (Kocher and Corti, 1951). These authors also found pantothenic acid (40 mg./kg. dry weight) and pyridoxin (traces up to 7 mg./kg. dry weight in activated sludge. Roulet (1948) and Roulet and Schopfer (1950) list references to the occurrence of pyridoxine and *p*-aminobenzoic acid in soil.

## PARTIALLY CHARACTERIZED COMPOUNDS FROM LAKES AND OCEANS

Mention will be made in this section only of fractions whose chemical identity is so poorly known that they cannot be placed in general chemical classes of compounds at the present time. Plankton toxins are discussed separately under the next heading.

SESTON. Lane (1950) obtained a chromatographic fraction from marine zooplankton oil which showed maximal light absorption at 310 mμ and was vitamin A-active to the fish *Limanda ferruginea*. Becking *et al.* (1927) obtained a crystalline precipitate from a chloroform–benzene extract of marine seston rich in the diatom, *Aulodiscus kittoni*. The material melted at 115°C., was slightly yellow in colour and liberated $H_2S$ on acidification.

WATER. Harvey (1925) obtained data suggestive of the presence of an organic Fe compound(s) in deep sea water. This compound(s) catalyzed the decomposition of added $H_2O_2$. In addition, his data suggested the presence of easily hydrolyzable inhibitors to this reaction in inshore waters. Keilin (see Harvey, 1925) suggested that the active factors were catalases and oxidases dissolved in sea water (see the section on enzymes).

Organic growth substances for the diatom *Ditylum brightwelli* were reported to be present in sea water by Harvey (1939). Two groups of substances were

found: A and N. The A group (adsorbed on carbon, insoluble in aqueous butanol) was apparently an ester(s) which liberated acid on hydrolysis. The A group was replaceable by cystine, glutathione, biotin and to lesser extent by thiamin. In this connection it is important to note the importance of SH groups in silicon metabolism of diatoms (J. C. Lewin, 1954). The N group (not adsorbed on carbon, soluble in aqueous butanol) was replaceable by a number of organic compounds including alanine, lactose and dextrose. The N group was destroyed by ashing or boiling in acid alcohol.

Kalle (1949) found two groups of substances in the dissolved (colloidal?) organic matter of sea water. He termed these fluorescent matter (pale blue fluorescence in ultraviolet light) and yellow matter. Johnston (1955) reported something similar to Kalle's yellow matter in sea water, and also the presence of several ultraviolet-fluorescing materials.

Lucas (1949), in a review of the ecological importance of external metabolites, mentions the importance of odours. Natural stream odours can be detected by the blunt-nosed minnow, *Hyborhynchus notatus*, as shown by Hasler and Wisby (1951). The odorous substances (to the fish) were lost on boiling, but could be concentrated by vacuum distillation. Hasler (1954) has reviewed the mechanisms and ecological importance of odour discrimination by fish.

Rodhe (1948, p. 79) found evidence of an organic factor in bacteria-free lake water which lowered the phosphate requirements of *Asterionella*. A knowledge of the chemical nature of this factor(s) might be useful in studies of productivity and algal culture.

Substances of an antibiotic nature appear to be present in the dissolved organic matter of both lakes and oceans. The ecological importance of these factors has been stressed by Lucas (1947, 1949), Lefèvre and Nisbet (1948), Lefèvre, Jakob and Nisbet (1952), Rice (1954) and Ryther (1954). Pratt (1942), and Pratt *et al.* (1944) found that a heat-labile, dialyzable substance(s) was produced in the culture medium of *Chlorella vulgaris*. This substance, later termed chlorellin, was inhibitory to the growth of *Chlorella*. Spoehr *et al.* (1949) have studied chlorellin production in considerable detail. Their data suggest that chlorellin is a mixture of partially oxidized unsaturated fatty acids. Healthy cells grown under $CO_2$ did not contain any chlorellin activity if fresh. Cells exposed to air for increasing periods of time showed an increased antibiotic effect. Rice (1954) found that *Chlorella vulgaris* and *Nitzschia frustulum* each produced a factor inhibitory to the growth of the other. Rice also found a factor of similar nature (passing through a Berkefeld filter and retained on Norit A) in the water of a natural *Pandorina* bloom; however, the toxicity was not demonstrated to be absent before the bloom.

Algal production of antibiotic substances is by no means restricted to *Chlorella*. Lefèvre, Jakob and Nisbet (1951) reported that water from an *Aphanizomenon* bloom inhibited the growth of other algae, and similarly for a bloom of *Oscillatoria planktonica*. These substances were found to be unstable to boiling. In this connection, Flint and Moreland (1946) reported earlier that cultures of blue-green algae produced extracellular substances lethal to other algae. The

production of antibiotics by algae has been most extensively studied and reviewed by Lefèvre, Jakob and Nisbet (1952). These workers have admirably succeeded in demonstrating the production of auto- and hetero-antagonistic agents both by laboratory cultures and by natural collections of a variety of algae. The chemical factors concerned have not been identified, but they can be concentrated by adsorption on activated charcoal.

Ryther (1954) found that substances produced by algae (one of which was *Chlorella*) inhibited the filtering rates of *Daphnia*. These substances were partly present in the water, but the greatest effects appeared to come through material liberated from the algae in the gut of *Daphnia*.

River water was found by Bogolyubov (1946) to contain an antibacterial substance. Denffer (1948) found evidence of a mitosis-blocking antibiotic in the used culture medium of *Nitzschia palea*. It has been suggested that the antibiotics produced by *Stichococcus bacillaris* and *Protosiphon botryoides* may be unsaturated fatty acids (Harder and Oppermann, 1953). Steemann-Nielsen (1955) reports that organic production rates as measured by $O_2$ production in light and dark bottles are in error because algae liberate anti-bacterial substances to the water, thus lowering the rate of bacterial respiration.

Berkefeld-filtered water from the English Channel apparently contains something inhibitory to the normal development of *Echinus*, *Ophelia* and *Sabellaria* larvae (Wilson, 1951). The factor(s) can be concentrated by adsorption on activated charcoal, and eluted with acetone (Wilson and Armstrong, 1952, 1954).

The nature of the compounds present in surface slicks on lake and ocean waters is unknown. It is known, however, that substances do exist which bring about marked lowerings of surface tension in certain areas (Adam, 1937; Hardman, 1941). (See also Addendum.)

SEDIMENT. Torstensson, Eriksson and Wicklander (1939) noted the presence of ultraviolet-fluorescing substances in sodium oxalate extracts of gyttja. Koe, Fox and Zechmeister (1950) separated four chromatographic fractions of ultraviolet-fluorescing substances present in methanol–petroleum ether extracts of marine sediments. These were characterized by their spectra (absorption peaks in the lower ultraviolet). Later work by Petracek, Fox and Zechmeister (1951) revealed four additional substances of similar nature, each characterized by chromatographic position and spectrum.

Vardabasso (1929) isolated an ether-soluble opalescent liquid (b.p. 150°C.) from Black Sea sediment. From its pungent odour it was presumed to be a thioderivative of an unsaturated aliphatic hydrocarbon. Small lumps of partly crystalline lipoid were found by Rolin (1942) in beach mud. The material melted at 58 to 61°C. and contained 75% C, 11.8% H, 12.5% O with smaller amount of S and N.

Although antibiotics are doubtless present in sediments, I have found only one reference to their occurrence there. Volkova and Shinkarenko (1946) found that an acidified ethanol extract of mud (freshwater?) was toxic to *Staphylococcus*.

The occurrence of floating sand on lake and sea surfaces appears to be a common phenomenon (Gates, 1926; Juday, 1926; Wilson, 1952). The causes of sand floatation may be due to electrical surface charges or surface tension phenomena brought about by the sand particles themselves or the coatings which they possess. Roy (1929) and Fox, Isaacs and Corcoran (1952) refer to the presence of organic matter adsorbed on sand particles. Marine sands appear to contain organic substances which affect the rate and success of settling of marine worm larvae on the sands (Wilson, 1952, 1953a, 1953b, 1955). These substances are insoluble in the ordinary fat solvents and are associated with the property of floatation.

## TOXIC PLANKTON

Blue-green algal blooms in lakes have often proved to be the sources of toxins which may result in the deaths of domestic animals that have imbibed the water. The subject has been reviewed by Prescott (1948), Olson (1951) and Ingram and Prescott (1954). The causative algae appear to be *Microcystis flos-aquae, M. aeruginosa, M. toxica, Aphanizomenon flos-aquae, Gleotrichia pisum, G. echinulata, Coelosphaerium Kuetzingianum* and several species of *Anabaena* (Prescott, 1948; Louw, 1950; Olson, 1951). It is quite possible that there is more than one kind of toxin produced by blue-green algae, but the present data are not adequate to clearly suggest that more than one organic substance is involved. However, Prescott (1948) found that hydroxylamine was present in decomposing blue-green algae in quantities sufficient to kill fish.

For the purpose of the discussion below I shall adopt the unproved and questionable assumption that the toxin is a single organic substance. Not even the general identity of the toxin is known with certainty. It is clear, however, from the work of Wheeler, Lackey and Schott (1942), Olson (1951) and Shelubsky (1951) that the toxin is dialyzable, stable to boiling in neutral solution, non-volatile, soluble in water or 95% ethanol and insoluble in chloroform or ether. Wheeler, Lackey and Schott (1942) report that the toxin is unstable in boiling 1 *N* acid or alkali. Shelubsky (1951) was able to precipitate the toxin with phosphotungstic acid at pH 2, and redissolve it by adding $Ba(OH)_2$. Shelubsky further showed that the toxin was destroyed if kept in 0.5 *N* NaOH for 24 hours at 2°C. Deem and Thorpe (1939) demonstrated that the toxin was not neutralized by botulinus antitoxins, and also that poisoned animals were free of *Clostridium botulinum*. Shelubsky (1951) stated that the toxin was not active serologically either as an antigen or as a hapten. The toxin has recently been obtained from bacteria-free cultures of *Microcystis aeruginosa* by Hughes, Gorham and Zehnder (1955). The most active fraction yet isolated showed high light absorption from 210 to 290 m$\mu$, and was lethal to 20-g. mice at a dosage of 0.7 mg. (Olson, 1951). Tests for alkaloids were negative (Olson, 1951).

The data of Louw (1950) for the toxin produced by *Microcystis toxica* are in some respects contradictory to the information given above. Louw found that this toxin had alkaloidal properties. He prepared a hydrochloride salt of an active fraction (regenerated from a phosphotungtic acid precipitate). The HCl salt had a

mol. wt. of 220, and an empirical formula of $C_{10}H_{19}NO_2.HCl$. Louw observed that rabbits developed a marked immunity when given sublethal doses of the *Microcystis toxica* toxin. The whole problem of blue-green algal toxins appears to be chemically complex and warrants further study.

The marine dinoflagellate *Gonyaulax catenella* is known to produce a toxin. The properties of this toxin are in general similar to those of the blue-green algal toxin outlined above, but there is no evidence to show that they are both of similar structure. There is some evidence (Sommer, Whedon *et al.*, 1937) that two toxins may be present. The primary toxin was concentrated by adsorption on Norit A columns to a preparation which had 3.3 mouse units per g. (Sommer, Riegel *et al.*, 1948). A mouse unit was defined as the amount which on intraperitoneal injection would kill a 20-g. mouse in 15 minutes. The toxin was found to be soluble in water, methanol, ethanol, glacial acetic acid and aqueous acetone, but insoluble in butanol, chloroform, ether, toluene or ethyl acetate (Sommer, Monier *et al.*, 1948). During concentration procedures the toxin was accompanied by betaine. Sommer, Monnier *et al.* (1948) and Riegel *et al.* (1949) have therefore suggested that the toxin may be a quaternary ammonium base similar (but not identical) to betaine. Besides Norit A, the toxin is adsorbed by sand and Permutit (Sommer and Meyer, 1937). It is not known if the toxin occurs in the dissolved organic matter of sea water. Brongersma-Sanders (1948) has reviewed the marine occurrences of toxic plankton. She has termed such waters hypertrophic, and noted that they lead to the formation of sapropel.

A third and quite different type of toxin is produced by the flagellate *Prymnesium parvum*. This toxin is destroyed by boiling water (Shilo and Aschner, 1953; Sproston, 1946). It is non-dialyzable, sensitive to oxidation by hypochlorite or permanganate, and even sensitive to air oxidation to a small extent. It is reversibly inactivated at pH's below 7.5 (Shilo and Aschner, 1953). It is known to exist naturally in extracellular form and may be a protein (Shilo and Aschner, 1953). Shilo, Aschner and Shilo (1953) report that fishes and tadpoles are sensitive to the toxin, but not frogs. They suggest that the toxin may act through absorption by gills.

## ENZYMES

The occurrence of enzymes in the living organisms of lakes, oceans, sewage, activated sludge and soil goes without saying. The purpose of this section is to draw to the attention of hydrobiologists some provocative and controversial evidence which indicates that free enzymes (i.e. not present in living organisms) may be important in chemical transformations in both lakes and oceans. Most of the evidence is based on the breakdown of a compound added to a freshly collected sample in the presence of toluene or after filter-sterilization. In many cases the sterility of the treated samples was not checked after the experimental run, and the low enzyme activities reported could be accounted for either by incomplete sterilization, contamination or perhaps even utilization of toluene by living organisms in toluene-treated samples. Toluene is known to be an ineffective sterilizing agent for wet soils and often not completely effective even for dry

soils (Subrahmanyan, 1927a, 1927b). ZoBell (1946) points out that toluene can be attacked by soil bacteria. In cases where enzymatic activity is measured by oxygen consumption, care must be taken to be sure that the oxygen-absorbing reactions are not purely chemical. Another point to be careful of when making comparisons of free enzyme as compared to living organism breakdown is that flasks of identical surface/volume ratios be used, since bacteria, and probably enzymes as well, are more active in dilute nutrient solutions the higher the ratio of surface to volume (ZoBell and Anderson, 1936; ZoBell, 1943). Another difficulty is that the various sterilization techniques may liberate enzymes from organisms—i.e. enzymes which were not originally free in the sample.

To be more certain that a specific reaction is brought about by a free enzyme, the methods of protein precipitation, concentration and denaturation should be used on the preparation to test whether the activity of the preparation is due to a protein. With the exception of a deaminating enzyme isolated from soil by Subrahmanyan (1927a, 1927b) no naturally occurring free enzyme appears to have been concentrated or partially purified.

The criteria to be adopted for the demonstration of a free enzyme are three in number:

1. That it has not arisen from the extraction of living organisms during the laboratory procedure.
2. That it can be concentrated, and exhibits properties of proteins (precipitations, denaturation, etc.).
3. That the specificity of reaction (substrates, inhibitors, pH dependence, etc.) is typical of a known enzyme.

The first criterion is perhaps the most difficult to document, except for water-soluble substances which pass through bacterial filters. Without these three criteria, the demonstration of free enzymes in nature must always be suggestive at the best.

WATER. Fermi (1906) found evidence of proteolytic enzymes in stagnant waters of pools, as well as in soils. Harvey (1925) first drew attention to the possible presence of free enzymes in sea water, although their presence in dead detritus was previously suggested, apparently without experimental evidence, by Pereira (1924). Harvey found that deep sea water decomposed added $H_2O_2$ faster than surface or inshore water. The rate of decomposition was found to vary with alkalinity and pH, could be inhibited by cyanide, but was not inhibited in the presence of $HgCl_2$. Activity was not lost by boiling unless a precipitate of $Mg(OH)_2$ formed. These data, plus the fact that sea water boiled with $HNO_3$ liberated some Fe, led Harvey to suggest, with Keilin's approval (see Harvey, 1925), that the active compounds might be catalases and oxidases.

The decomposition of added $H_2O_2$ by mineral waters is influenced by a variety of electrolytes (Mougeot and Aubertot, 1928; Frenkel, 1929), and it seems possible that variations in the concentration of electrolytes in sea water might be the basis of Harvey's results. Matsudaira (1950) has shown that sea-water decomposition of $H_2O_2$ is influenced by chlorinity. Matsudaira suggested

that the $H_2O_2$-decomposing activity of sea water is largely due to the $Cl^-$ ion rather than an enzyme or organic-Fe compound. Matsudaira found that the activities of his samples of sea water were not lowered by boiling, evaporation or ignition. It is not possible to reach any conclusion from these two conflicting papers (Harvey, 1925; Matsudaira, 1950), but in view of the scanty evidence provided by Harvey, his suggestion must be taken with a grain of salt.

Kreps (1934), in a little known paper, reported that nitrate reduction and ammonia oxidation in $HgCl_2$-treated or Seitz-filtered sea water showed little difference as compared to untreated controls. He suggested the importance of free enzymes in organic-matter transformations in sea water and thought that such reactions might be particularly important in bottom waters and muds. Similar evidence of free enzymes in sea water was given by Keys, Christiansen and Krogh (1935) and Bokova *et al.* (1936). It is noteworthy, however, that Waksman and Carey (1935a) reported that one sample of Seitz-filtered, sterile sea water showed no oxygen absorption in 5 days at 20 to 22°C. in the dark.

SEDIMENTS. ZoBell (1939) found that toluene- or $HgCl_2$-treated marine mud slowly absorbed oxygen from oxygen-saturated water. The types of change were separated into chemical, enzymatic and respiratory (living cells). Each type was shown to exist. Messineva (1940) reported the occurrence of catalases, peroxidases any proteolytic enzymes in river muds, the concentrations decreasing with depth below the mud surface. Messineva suggested that bacterial enzymes may operate in muds after the death of the bacteria which produced them. Whitehead and Breger (1950) suggested that marine mud may possess catalysts active in hydrocarbon formation at temperatures of 135°C. and lower. Their nature is unknown, but they are probably not enzymatic.

SEWAGE. Free enzymes in sewage and activated sludge have not been demonstrated; however, some of the data of Wooldridge and Standfast (1932, 1936) and Ingols (1939) are suggestive in that direction.

SOIL. Urease-like activity in soil has been reported by Conrad (1940a, 1940b, 1942), Hofmann and Seegerer (1951) and Hofmann and Schmidt (1953). Ammonia-forming enzymes were found in soil by Russell and Hutchinson (1909) and dephosphorylating enzymes by Rogers (1942). In no case, however, have the primary data been sufficient to point unequivocally to free enzymes.

Subrahmanyan (1927a, 1927b) partly purified a deaminating enzyme from soil by aqueous glycerol extraction and ethanol precipitation. It was not proved that the enzyme occurred free in soil.

## CONCLUDING REMARKS

Having revealed the extent of our ignorance about the molecular nature of organic matter in lakes, oceans, sewage and soil, one can only hope that this may help to focus the critical eye on overlooked aspects of ecology and biochemistry. Complete coverage of the literature has not been achieved. I feel, however, that

more than 80% of the important papers have been included. It is not feasible at the present time to suggest any tentative general conclusions except that this is a wide-open field for future research.

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## ADDENDUM

Several important papers have been seen since the original manuscript was submitted for publication. Corti (*Schweiz. Z. Hydrol.*, **15**: 152–157; 1953) has identified 16 amino acids in hydrolysates of activated sludge. Pillai, Rao, Mohan, Krishnamurthy and Prabhakara (*Current Sci.* (India), **22**: 235; 1953) simultaneously presented similar data, and in addition showed that most of the amino acids also occurred in the free state, although in markedly lower concentrations. Erdman, Marlett and Hanson (*Science*, **124**: 1026; 1956) have performed the first analysis of amino acids in marine sediments. Using paper chromatography, valine, alanine, glutamic acid, aspartic acid, leucine and/or isoleucine, glycine, proline, tyrosine, phenylalanine and arginine (?) were identified in a hydrolysate of a late Pleistocene marine mud.

A basic study of the changes of chlorophyll concentration in light and dark bottles by Marshall (*J. Mar. Res.*, **15**: 14–32; 1956) revealed some unexpected results: in certain cases there was an increased amount of chlorophyll in dark bottles, while in others a decline in chlorophyll was observed in light bottles, even during population growth. These data have important bearing on the validity of the pigment methods for assaying phytoplankton populations, though perhaps only in poorly mixed environments.

With regard to soils, Bremner (*Z. Pflanzenernähr. Bodenk.*, **69**: 32–38; 1955) refers to unpublished work by Morrison showing that vanillin, syringaldehyde and *p*-hydroxybenzene are produced by alkaline nitrobenzene oxidation of soil humic acids. The quantities produced were less than 1/25 of those produced by fresh lignin under similar treatment, suggesting a drastic modification of lignin during the formation of soil organic matter. Wrenshall and McKibbin (*Canad. J. Res.*, B, **15**: 475–479; 1937), in an overlooked paper, reported the isolation of adenine and uracil from soil hydrolysates. Uracil had not been detected previously in terrestrial soil.

It is of interest to note that Provasoli and Pintner (*Proc. Soc. Protozoologists*, **4**: 10; 1953) reported concentrations of vitamin $B_{12}$ in sea water ranging from 0.03 to 0.2 $\mu$g./l. These values are markedly higher than those reported by Droop and Lewin (see the section on vitamins). In the present state of meagre knowledge it is difficult to know whether the discrepancy is due to the different methods used or to local and seasonal variation in the vitamin $B_{12}$ content of sea water.

Finally, an important paper by Cheesman (*Nature*, Lond., **178**: 987–988; 1956) shows that at least one species of snail (*Pomacea canaliculata*) is capable of concentrating and eating the surface film of protein on water by using its foot as a Langmuir trough. This noteworthy finding may create a renewed interest in the nature of surface slicks on lakes and oceans and their role in food cycles.

# The Smaller Cetacea of Eastern Canadian Waters[1]

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## ABSTRACT

An account is given of the known records, distribution and migrations of the smaller Odontocete whales occurring in eastern Canadian waters, with measurements of specimens obtained of the rarer species. The distribution of the abundant pilot whale *Globicephala melaena* (Traill) has been studied in most detail. The species' summer range includes both the offshore waters of the Labrador Sea and the coastal waters around Newfoundland. The coastal population feeds only on the squid *Illex illecebrosus* (LeSueur) and its movements inshore in spring and offshore in autumn follow those of the squid over the southwest Grand Bank. In some years a failure of the squid to move shorewards results in a failure of the fisheries for both squid and pilot whales in Newfoundland. The species is known to winter in an oceanic area southeast of the Grand Bank.

The white-sided dolphin *Lagenorhynchus acutus* Gray associates with the pilot whale and apparently inhabits the same climatic zone in these waters, while the white-beaked dolphin *L. albirostris* Gray is found in somewhat colder waters. The killer whale *Grampus orca* (L.) migrates northwards in spring along the Newfoundland and Labrador coasts, its migration coinciding with that of the rorquals.

New records for the waters of eastern Canada, extending the known range of each, are given for *Mesoplodon bidens, Tursiops truncatus, Lagenorhynchus albirostris* and *Lagenorhynchus acutus.*

## INTRODUCTION

THIS paper describes the records, abundance, distribution and migrations of the smaller whales found in the inshore and offshore waters around the Maritime Provinces, Newfoundland and Labrador, with some reference to those recorded from the Quebec shores of the Gulf of St. Lawrence. Only the small Odontocetes from these waters are described. The sperm whale, *Physeter catodon* L., and the large whalebone whales will be treated in a separate paper.

The more recent accounts of the cetacean fauna of these waters have been lists only: Anderson (1946) listed known Canadian species and Miller and Kellogg (1955) listed North American species in general, together with all other mammals. We have been able to add several new species to the Canadian list, including some of those predicted by Anderson. In addition, for some species such as the pilot whale *Globicephala melaena* (Traill), we have gathered new knowledge about the offshore distribution. Since the pilot whale supports a considerable small-whaling industry in Newfoundland this knowledge is of some economic importance as well as of zoological interest.

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## SOURCES OF INFORMATION

This paper is a compendium of our own observations, those made by other workers at the Biological Stations of the Fisheries Research Board of Canada at St. John's, Newfoundland, and St. Andrews, N.B., and of other observers, particularly personnel of the United States Coast Guard. Published records are also cited to complete the account as far as possible.

Inshore records have come from casual observations from 1949–54 by Fisher in the Maritimes, particularly in Passamaquoddy Bay, and three summers' observations (1952–54) by Sergeant in Trinity and Conception Bays on the east coast of Newfoundland. Catches made by the small-whaling industry situated at Dildo near the head of Trinity Bay have furnished records from the beginning of the industry in 1947 until the time of writing. Elsewhere in the Maritime Provinces, Quebec and Newfoundland occasional strandings have been reported in the press or in scientific papers, or have been observed by personnel of the Stations or reported to them.

For waters off the coast and over the Continental Shelf, records have come from personnel of the two Biological Stations working on research vessels and commercial fishing vessels. Questionnaires were issued by Sergeant in 1953 and 1954 with attached aids to identification of expected species. The main purpose of the questionnaire was to trace the seasonal distribution and abundance of pilot whales, but other Cetacea were also recorded. Some records from coastal waters entered on these questionnaires have also come from personnel of the United States Coast Guard as described below. Mr. Malcolm S. Gordon of Yale University kindly made available his records of Cetacea seen along the coast of Labrador during summer cruises of the schooner *Blue Dolphin* in 1951 and 1954. These notes are especially valuable since little other information from the Labrador was available to us. Some records have come independently also from officers of draggers operating out of St. John's.

The investigation was extended to include waters outside the Continental Shelf through the co-operation of the United States Coast Guard, who kindly arranged for personnel of their ships to make observations at weather stations in the northwest Atlantic (Fig. 1). Observations were recorded on the same questionnaires as those used in Newfoundland. From June 1953 to June 1954 very complete observations were received in this way from Station "B", or "BRAVO", situated at approximately 56°45′N. Lat., 51°00′W. Long., in the Labrador Sea, and between this region and the Newfoundland and Labrador coasts while ships were proceeding to or from Station. From July 1954 to July 1955 observations were received from Station "D", or "DELTA", situated east of the Grand Bank at approximately 44°00′N., 41°00′W., and between this region and the North American coast.

In general there has been no difficulty in interpreting identifications of whales and porpoises where precise enough descriptions were given. The small number of species met with in cold water regions, like those around Newfoundland and at Station "B" made interpretation generally easy, but a number of

Cetacea recorded in the warmer water at Station "D" remained mysteries. Doubtful records were of course discarded. Many good descriptions of appearance and behaviour were received on the questionnaires or on attached notes, and two photographs sent in by one Coast Guard observer confirmed his identification of pilot whales.

In the systematic account the nomenclature and order followed is that of Miller and Kellogg. Vernacular names used in Newfoundland follow the usual English names. Discussion of data takes place in the account of each species.

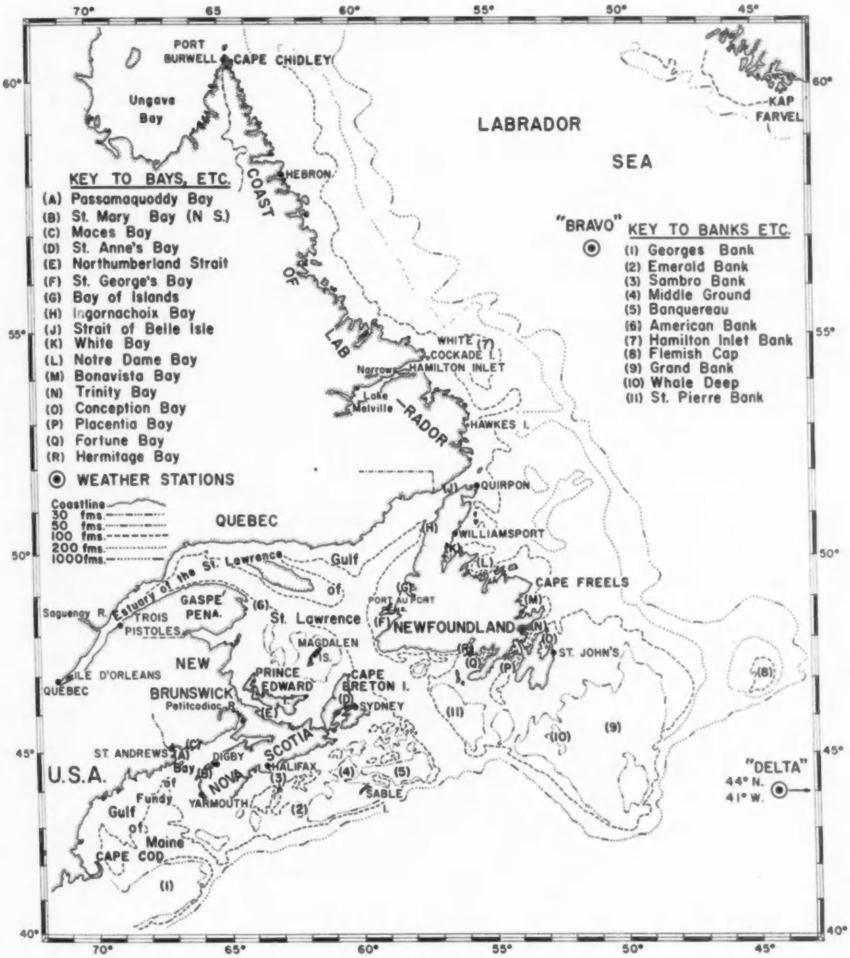


FIGURE 1.—Map showing principal place-names mentioned in text.

## HYDROGRAPHIC CONDITIONS

A good general account of the hydrography of the area covered in this paper is that of Hachey, Hermann and Bailey (1954). The following summary refers chiefly to surface water temperatures.

The coastal surface waters from the Gulf of Maine to the mid-Labrador coast are characterized by marked seasonal changes in temperature; the offshore waters, in contrast, both at Station "D" in the North Atlantic Current and Station "B" in the Labrador Seat have much more equable temperatures throughout the year.

The waters off the south coast of Nova Scotia comprise three distinct oceanographical regions: coastal waters, "slope water" and Gulf Stream waters. The coastal waters are in the main cool, the surface layer varying in temperature with the seasons approximately between –1°C. and 20°C. The "slope water" is a well-defined band of mixed water lying between the coastal waters and the Gulf Stream. It is formed by the large-scale mixing which occurs in the area of confluence of the Labrador Current and the Gulf Stream in the southwest part of the Grand Bank and westward. The warm and highly saline Gulf Stream waters pass the area well offshore. At Station "D" we have no regular temperature records, but a Coast Guard observer has recorded surface temperatures of 20°C. on June 30 and 21°C. on July 2, 1954, and data published by the International Council for the Exploration of the Sea show temperatures of 23°C. in August in this general area.

The waters of the Bay of Fundy are well-mixed and show a seasonal cyclic variation in temperature and salinity, which is less extreme than that of the coastal waters off Nova Scotia. Surface waters vary from a mean of 1.5°C. in March to a high of 11.5°C. or more in September.

The east coast of Newfoundland receives the coastal branch of the Labrador Current, and the yearly variation in temperature of the surface waters is from a minimum in February and March of below –1°C. to a maximum in August-September of about 16°C. Drift ice in recent years has normally reached as far south as the mouth of Trinity Bay from about late March to late April, and strings of ice may pass down the Avalon Peninsula and block Trinity and Conception Bays, as in April 1953 and May 1955.

The offshore surface waters of the mid-Labrador Sea, as studied at Station "B" and reported by Kielhorn (1952), have a yearly temperature variation of from 3° to 9°C. With these limits and range they resemble waters of the Northeast Atlantic, in the latitude of the Faeroe Islands or the north-central Norwegian coast.

## SYSTEMATIC ACCOUNT

### Family ZIPHIIDAE. Beaked whales

***Mesoplodon bidens*** (Sowerby). Sowerby's beaked whale.

A male 15 ft. 6 in. (472 cm.) in length was examined by Sergeant at Chapel Arm, Trinity Bay, Newfoundland, on August 26, 1952. It had been pulled ashore

TABLE I.—Body measurements and other data of specimens mentioned in the text. All measurements in centimetres.

| | *Mesoplodon bidens* | *M. bidens* | *Delphinus delphis* | *D. delphis* | *Tursiops truncatus* | *Lagenorhynchus acutus* | *L. acutus* |
|---|---|---|---|---|---|---|---|
| Species / Locality | Trinity Bay, Nfld. | Wild Bight, Nfld. | Sambro & Emerald Banks | Middle Ground Band | Petitcodiac R., N.B. | Trinity Bay, Nfld. | Trinity Bay, Nfld. |
| Date | Aug. 25, 1952 | Sept. 25, 1953 | Aug. 21, 1954 | Oct. 22, 1954 | Sept. 15, 1950 | July 30, 1954 | July 30, 1954 |
| Sex | ♂ | ♀ | ♀ | ♂ | ♀ | ♂ | ♂ |
| 1. Standard length, tip of snout to notch of flukes | 472 | ca. 427 | 218 | 204 | 249 | 180 | 150 |
| 2. Tip of snout to slit of blowhole | 56 | 55 | ... | 33 | 35 | 31 | 29 |
| 3. Tip of snout to angle of mouth | 36 | 28 | 28 | 26 | 29 | ... | ... |
| 4. Tip of snout to centre of eye | 60 | 56 | ... | 31 | 34 | 29 | 27 |
| 5. Tip of snout to anterior insertion of flipper | 15 | ... | ... | 46 | 53 | ... | ... |
| 6. Centre of eye to centre of ear | ... | ... | ... | ... | 11 | 5 | 6 |
| 7. Reproductive aperture to anus | ... | ... | ... | 15 | ... | ... | ... |
| 8. Anus to notch of tail flukes | ... | ... | ... | 57 | 64 | ... | ... |
| 9. Flukes, total spread | ... | ... | ... | 50 | 48 | ... | ... |
| 10. Notch of flukes to posterior border of dorsal fin | 162 | ... | ... | 102 | ... | ... | ... |
| 11. Dorsal fin, length at base | 15 | ... | ... | 36 | ... | ... | ... |
| 12. Dorsal fin, greatest vertical height | 20 | ... | ... | 22 | 20 | ... | ... |
| 13. Flipper, axilla to tip | 36 | ... | ... | 26 | 24 | ... | ... |
| 14. Flipper, anterior border to tip | 48 | ... | ... | ... | ... | ... | ... |
| 15. Flipper, greatest width | 16 | ... | ... | 11 | 12 | ... | ... |
| 16. Head, occipital condyles to tip of snout | ... | ... | ... | ... | ... | 45 | 39 |
| 17. Projection of lower jaw beyond snout | ... | 0.65 | ... | ... | 1.0 | ... | ... |
| 18. Length of beak | ... | ... | 14.6 | 12.7 | ... | ... | ... |
| 19. Girth at level of axilla | 254 | ... | ... | ... | 102 | ... | ... |
| 20. Girth at level of anterior end of dorsal fin | 239 | ... | ... | ... | ... | ... | ... |
| 21. Tooth count: L = left, R = right | $L\frac{0}{1}$ $R\frac{0a}{1}$ | $L\frac{0}{0}$ $R\frac{0a}{0}$ <br> $L\frac{0}{1}$ $R\frac{0b}{1}$ | $L\frac{45}{49}$ $R\frac{47c}{50}$ | $L\frac{42}{47}$ $R\frac{40b}{46}$ <br> $L\frac{46}{46}$ $R\frac{45c}{46}$ | $L\frac{24\text{-}25}{25}$ <br> $R\frac{24\text{-}25c}{25}$ | ... | ... |

[a]No rows of small teeth as reported by Boschma (1951) were noted.
[b]In fresh specimen.
[c]In skull.

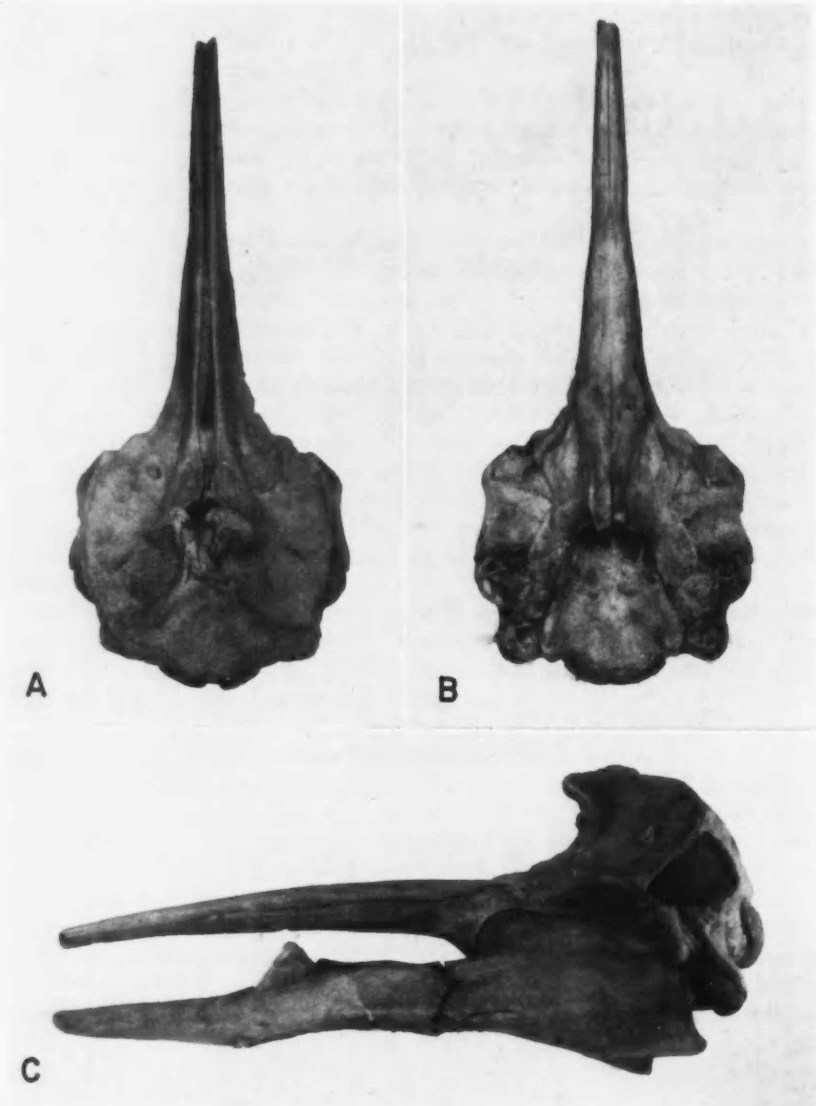


FIGURE 2.–*Mesoplodon bidens*. A, dorsal; B, ventral; and C, lateral views of skull of male.

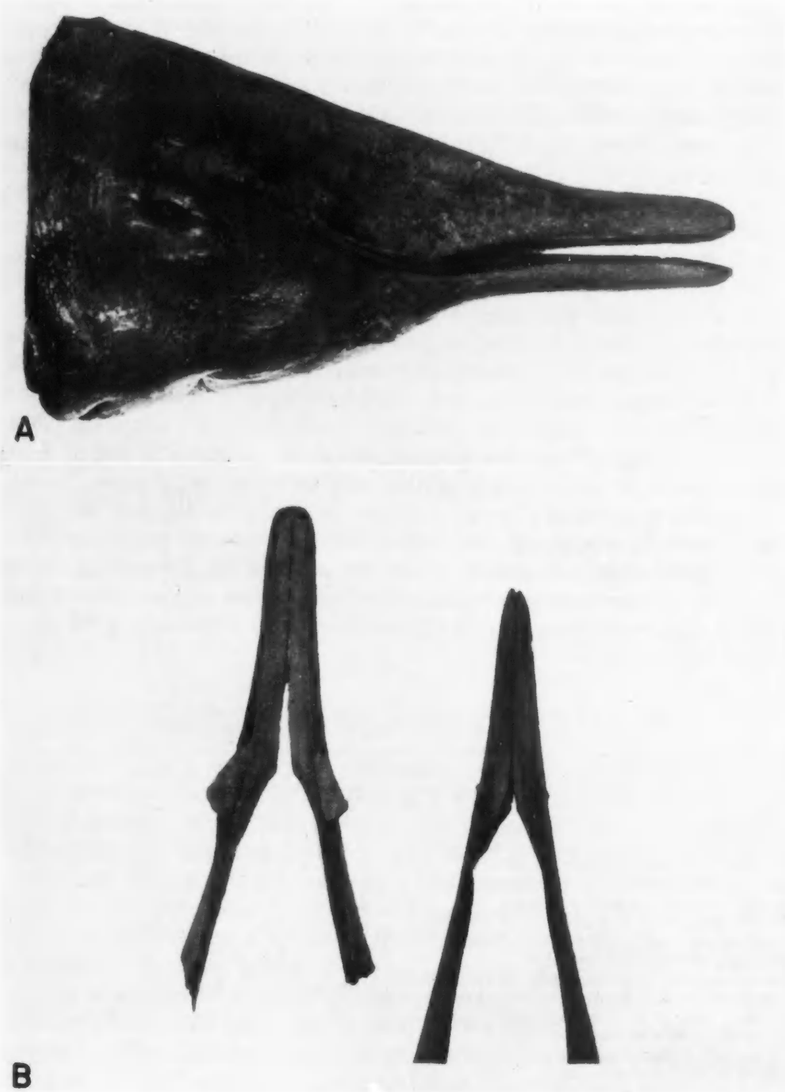


FIGURE 3.—*Mesoplodon bidens.* A. Lateral view of head of female. B. Dorsal view of lower jaws of male, left, and female, right, to show teeth.

by fishermen immediately after a drive of pilot whales, but was judged some two days dead and bore no lance wounds as the pilot whales did. It had thus apparently stranded independently of them. Sketches and a rough dissection were made immediately, and the skull was cleaned and preserved. This is seen in Figure 2. Identification was later confirmed by comparing photographs of the skull with skulls of *Mesoplodon* in the collection of the British Museum, Natural History, with the help of Dr. F. C. Fraser. This type of whale was quite unknown to the fishermen.

A second specimen was harpooned at Wild Bight, Notre Dame Bay, Newfoundland, on September 23, 1953. The head together with a drawing and description were sent to the St. John's Station of the Fisheries Research Board by Mr. James Strong of Little Bay Islands, and the skull was preserved. The length of the animal was given as 14 ft. (about 430 cm.). The teeth had not pierced the gums (Fig. 3). The teeth of Ziphiids erupt only in adult males. The large size, small teeth and absence of protruding teeth in the gum suggest that the animal was a female. The two skulls are now in the collection of the National Museum of Canada at Ottawa.

Measurements of the male specimen are shown in Table I, and of the two skulls in Table II. Other details of the male specimen noted were: "colour a uniform slate-grey dorsally, possibly lighter on the underside, but skin too decayed to show colour clearly. Scars of tooth-marks all over body. Teeth about centrally placed between apex of snout and angle of jaw, projecting one inch above gum, both with a stalked barnacle (*Conchoderma* sp.) attached. Stomach empty. Hind-gut running straight and dorsally. Testes . . . measuring 7.5 cm. long by 3 cm. in diameter".

TABLE II.—Measurements of the two skulls of *Mesoplodon bidens* (Sowerby) mentioned in the text.

| Dimension | Male | Female |
|---|---|---|
| | *mm.* | *mm.* |
| Condylobasal length | 740+ | 450+ |
| Height, vertex to inferior border of pterygoids | 265 | 235 |
| Breadth across middle of pterygoids | 295 | 270 |
| Breadth across postorbital processes | 315 | 290 |
| Breadth across zygomatic processes | 300 | 270 |
| Breadth of rostrum at base | 202 | 184 |
| Length of premaxilla | 605+ | . . . |
| Breadth of premaxilla at middle | 40 | 43 |
| Greatest breadth of premaxilla in front of nares | 104 | 100 |
| Greatest breadth of premaxilla behind nares | 103 | 98 |
| Length of portion of vomer visible on palate | 155 | 185 |
| Greatest length of nasals | 33 | 28 |
| Greatest breadth of nasals | 35 | 40 |
| Breadth of anterior nares | 51 | 48 |
| Breadth of occipital condyles | 113 | . . . |
| Breadth of each condyle | 39 | . . . |
| Breadth of foramen magnum | 41 | . . . |
| Length of mandible | 665 | 593 |
| Height at coronoid process | 103 | 99 |
| Distance from tip of jaw to centre of tooth | 63 | 35 |
| Ventral face of mandible to apex of tooth crown | 92 | 50 |
| Length of symphysis | 235 | 195 |

Although Anderson predicted the occurrence of *M. bidens* in eastern Canadian waters, these are the first definite records. Some thirty stranded specimens have been recorded from northern Europe and one from the eastern United States, at Nantucket Island, Massachusetts (Allen, 1906). For three records cited in Allen's paper, but later referred to other species, see True (1910). Our two records in two summers suggest that the normal summering range of the species may lie in boreal offshore waters, and that occasional specimens may be attracted to the Newfoundland coast by the dense stocks of squid *Illex illecebrosus* (LeSueur) found there.

***Mesoplodon densirostris*** (Blainville)

We have not seen this whale ourselves, but Raven (1942) records an adult male, length 14 ft. 5 in. (439 cm.) taken at Peggy's Cove, Nova Scotia, on February 4, 1940. The skeleton is now in the American Museum of Natural History. There are four additional records from the United States coast from North Carolina to Massachusetts.

***Mesoplodon mirus*** (True)

This species was recorded from South Gut, St. Anne's Bay, Cape Breton Island, on August 5, 1938 (Allen 1939). The skeleton is now in the Museum of Comparative Zoology at Harvard. We have not encountered the species. There are six or more records from the United States coast from North Carolina to Maine.

***Hyperoodon ampullatus*** (Foster). Bottlenose whale

A male, length about 22 ft. (670 cm.), was taken at Dildo Arm, Trinity Bay, Newfoundland, on July 27, 1953. A companion escaped and was seen in the southern part of the bay for three days thereafter. These whales were not seen by Sergeant, but from their size and from the description given by Captain Iver Iversen, an experienced Norwegian whaling captain, there can be no doubt of the identification. There is a previous Canadian record: a female, length 22 ft. 1 in. (673 cm.), taken at Cap Martin in the estuary of the St. Lawrence, Quebec, on September 4, 1940 (Beaugé, 1941).

The Dundee whalers knew of the occurrence of bottlenose in the entrance of Hudson Strait, and prosecuted a small fishery there on their way north from the Newfoundland sealing to the summer hunting of right whales. Lindsay (1911) describes how the ship on which he sailed in 1884 took two bottlenose from a school well off Cape Chidley, and one from another school off Frobisher Bay.

According to Murray and Hjort (1912) bottlenose whales feed on the arctic squid *Gonatus fabricii* (Fabricius). This is a species of subarctic waters, the young of which frequently occur in Labrador Current waters south to the vicinity of Newfoundland.

## Family KOGIIDAE. Pigmy sperm whales

### ***Kogia breviceps*** (Blainville). Pigmy sperm whale

We have not seen this whale ourselves, but a record was published by Piers (1923) of a female found dead under ice in the outer part of Halifax harbour on January 17, 1920. A full description and drawings were given by Piers.

## Family MONODONTIDAE. Narwhals and white whales

### ***Delphinapterus leucas*** (Pallas). White whale, beluga

A record of a lactating female white whale from Maces Bay on the New Brunswick side of the Bay of Fundy on June 12, 1952, has been published (Fisher and Sergeant, 1954). Almost every year fishermen report sighting one to several white whales in the Bay of Fundy. These probably represent offshoots of the well-known population found in the St. Lawrence estuary, and fully described by Vladykov (1944).

We have no certain records for Newfoundland, but a white porpoise, probably a white whale, was seen in Dildo Arm, Trinity Bay, in March several years ago by local fishermen, two of whom reported the occurrence independently to Sergeant from memory. There is also a report of a herd of "white squidhounds" seen among ice off nearby New Harbour in March. For neither record could the year be ascertained exactly, but both appeared to have come from 1938 or 1939. It is surprising that there are no more records, in view of the proximity of the St. Lawrence population, and of the flow of the Labrador Current from Arctic regions frequented by white whales. Vladykov, noting fluctuations in past catches in the St. Lawrence, thought that the population there might be replenished in cold years by immigrants from further north. However, he could find no precise records of white whales from the Labrador coasts; and we have none.

Two factors are suggested to account for this discontinuous distribution of white whales within our area. First, the fairly even low temperatures in the part of the estuary of the St. Lawrence frequented by white whales, and in the Bay of Fundy, are in contrast to the widely fluctuating surface temperatures of Labrador Current waters (Hachey *et al.*, 1954). Again, the estuarine conditions in these two areas contrast with the coasts of Newfoundland and Labrador. Newfoundland has no large estuaries and Labrador has only one, Lake Melville, which has a very narrow entrance. White whales enter estuaries in summer over much of their arctic range, though by no means all of it (see map on page 46 of Vladykov, 1944). The reasons for this are not clear; their food in summer consists both of anadromous fish and of marine animals such as capelin *Mallotus villosus*, squids, and bottom-living fish and invertebrates. The exact factors may be physiological or even historical rather than based on food.

## Family DELPHINIDAE. Porpoises and dolphins

### ***Delphinus delphis*** L. Common dolphin

Two adults, a female and a male, were harpooned off the east coast of Nova Scotia by Lt. G. C. Wicks from the Canadian Naval oceanographic research ship *Sackville,* on August 21 and October 22, 1954, respectively. Identification was confirmed by Dr. Remington Kellogg of the United States National Museum, where the skulls are deposited.

The female was taken between Sambro and Emerald Banks at approximately 43°30′N., 63°00′W. It was lactating, and was accompanied by a calf. Extensive schools of dolphins, apparently of the same species, were present. The stomach contained remains of billfish, *Scomberesox saurus* (Walbaum). The male was taken on Middle Ground Bank at approximately 44°00′N., 61°00′W. Extensive schools of dolphin were again present. The stomach was empty. Measurements of both specimens are shown in Table I.

Anderson states that this species is of casual occurrence in waters off the Maritime Provinces. The two specimens and the extensive schools described above were in the region of "slope water", and were taken at temperatures of between 13 and 17°C. Apparently the dolphins are numerous in this area off Nova Scotia during the late summer and autumn. The two records above are as far as we know the first specimen records for the localities involved.

### ***Tursiops truncatus*** (Montague). Bottlenosed dolphin

An immature female was taken alive from the Petitcodiac River at Salisbury, New Brunswick, about September 15, 1950, by P. F. Elson of the Fisheries Research Board's St. Andrews Station (Fig. 4A). The river at that point is little more than a stream, although within tidal influence. The animal had probably entered the river on a flood tide from the Bay of Fundy, and had been trapped in the shallows upriver. It was placed in a freezer and examined later by Fisher. Measurements available are given in Table I. So far as we know, this is the only definite record of this dolphin on the Atlantic coast of Canada, although its known range extends north to Maine (Miller and Kellogg, loc. cit.).

### ***Lagenorhynchus albirostris*** Gray. White-beaked dolphin.
Local name: Squidhound

Seven dolphins of this species came ashore at Seal Cove, Conception Bay, Newfoundland, on March 20, 1953 (Fig. 4B). They had been trapped by advancing sea ice, and were killed by local residents. Five were examined by H. J. Squires and E. L. Rowe of the St. John's Station. Four were males of lengths 211, 216, 224 and 239 cm., one a female of length 196 cm. (from 6 ft. 5 in. to 7 ft. 10 in.). Tooth counts of two animals gave dental formulae of $\frac{23\ 23}{24\ 24}$ for one and $\frac{22\ 22}{23\ 23}$ for the other. Stomach contents of two were bones of cod, and all had stomach

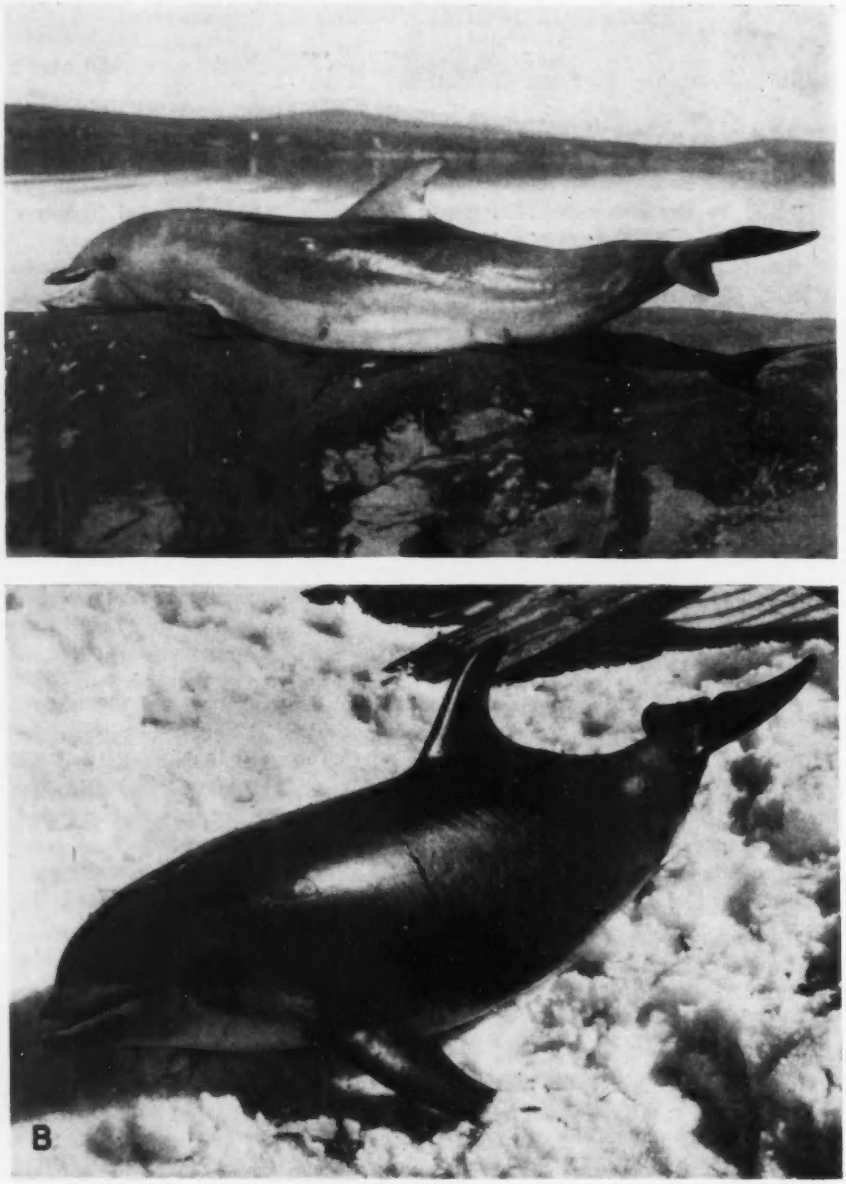


FIGURE 4.—A. *Tursiops truncatus*. Female, length 249 cm., Petitcodiac River, N.B., ca. September 15, 1950. B. *Lagenorhynchus albirostris*. Male, length 216 cm., Seal Cove, Newfoundland, March 2, 1953.

nematodes, probably a species of *Anisakis*. The skull of the male, length 216 cm., is now in the National Museum of Canada, Ottawa. Another specimen was harpooned from a herd of about six at Port de Grave, Conception Bay, Newfoundland, on May 10, 1954, by a fisherman, Mr. Lear. The head was obtained by Sergeant and the skull preserved; the sex is not known. A herd of twelve identified as this species was seen by Sergeant in southern Trinity Bay close to New Harbour on October 7, 1952. Features noted were: the relatively large size (as compared with *Lagenorhynchus acutus*), and the obscure grey markings of the sides. The dolphins were close to, but moved away independently of, a herd of pilot whales with a few *L. acutus*. A herd of about four was also seen by Sergeant in Dildo Arm, Trinity Bay, on November 10, 1953, just after the last pilot whales had disappeared. From Labrador, M. S. Gordon sends the following sight identifications: four to six south of White Cockade Island, northern Hamilton Inlet, on July 29, 1951, and a "small school" near the same island on August 12, 1951. Other sight records from various sources cannot definitely be assigned to this species.

Two "squidhounds" taken by the whalers in Dildo Arm, Trinity Bay, on September 8 and 10, 1948, may have been of this species. No description is available, but the length of the specimens, a male and a female, were both recorded as 10 ft. (250 cm.). This is within the range of *L. albirostris* but is large for *L. acutus*.

***Lagenorhynchus acutus*** White-sided dolphin. LOCAL NAME: Jumper

Two males, lengths 180 and 150 cm. (5 ft. 11 in. and 4 ft. 11 in.), were driven ashore with pilot whales at Chapel Arm, Trinity Bay, Newfoundland, on July 30, 1954. The larger was examined by Sergeant the next day after it had been partly flensed, and the skull obtained; this is now in the National Museum of Canada. The head of the second was obtained by C. A. Rose, who was present at the stranding. Measurements were taken on the head in a frozen state, but it was later lost. Measurements are shown in Table I. The stomach of the larger animal contained remains of squid *Illex illecebrosus* and herring *Clupea harengus* L. Its age was estimated from the teeth as about three years, and the testes were those of an immature or a non-breeding male. Identification confirmed numerous sight-records made in Trinity Bay in this and previous summers by Sergeant. This strikingly marked dolphin appears to visit inshore waters of Newfoundland in summer, often in company with pilot whales. Several times we have seen herds of these two species intermixed and probably feeding together on a shoal of squid, but when disturbed by our approaching boat the dolphins usually moved off in a separate group. In Trinity Bay white-sided dolphins are less numerous than pilot whales, and are much less commonly driven ashore. In about 50 drives of pilot whales witnessed by Sergeant, white-sided dolphins remained in company only twice, and on one of these occasions the six dolphins turned back at the last moment and escaped. On the second occasion, noted above, two out of a group of about six were killed with the

pilot whales. However, the fishermen who have driven whales for many years speak of having driven ashore large numbers of dolphins occasionally in the past; the numbers given were 200 to 250, but these are possibly exaggerations. We have a single sight-record from southern Labrador: a herd of 20 to 25 seen by M. S. Gordon 20 miles north of St. Lewis Sound on August 21, 1954.

Fairly certain records of white-sided dolphins offshore are: a herd of 15 to 20 from the southern part of the Grand Bank at 44°31'N., 52°15'W. on April 11, 1954 (A. Kelland, E. M. LeGrow), and 50 to 60, associated with pilot whales, at 56°28'N., 50°46'W., on August 4, 1953 (J. T. Allison, U.S.C.G.). Observers in both instances describe the dolphins as grey with a white stripe on the side. Sergeant also noted that the mid-lateral white stripe was a good field-character in dull light, when no other part of the colour pattern was discernible. Other sight-records of dolphins off the Newfoundland and Labrador coasts cannot be assigned to species, but most of them probably refer to one or other species of *Lagenorhynchus*. The herds usually consisted of 20 to 60 animals, and observers several times found them associating with pilot whales. Occasionally hundreds of dolphins were seen together, as at 50°25'N., 50°37'W. (northeast of Cape Freels, Newfoundland, on the edge of the Continental Shelf) on October 6, 1953, by A. Kelland and E. LeMessurier, and on the southern edge of the Grand Bank in January, 1953, when a vast concourse was seen by Capt. B. Blackwood of the trawler *Blue Spray*. Maxwell (1952) once found very large numbers of *L. acutus* massed together off the Outer Hebrides, while Norman and Fraser (1949) quote Beddard to the effect that very large numbers of *L. albirostris* have been seen together off the Norwegian coast.

In inshore waters of Newfoundland, as far as our observations go, we can distinguish the two ecologically by several features, as follows:

| Feature | *L. albirostris* | *L. acutus* |
|---|---|---|
| Time of occurrence | Spring and fall (at least March–May and October–November) | Summer (July to October) |
| Size of herd | Small, usually 6 to 8 | Medium, usually 40 to 50 |
| Associations | Alone | Often with pilot whales |

*L. albirostris* may thus be a species preferring colder waters than *L. acutus*. True (1889) recorded six skulls of *L. acutus* from the Cape Cod region in the collection of the U.S. National Museum, and Schevill (1956) recorded seeing a school of about a dozen and collecting one *L. acutus* 50 miles off Monomoy Point, Cape Cod, on September 14, 1954. In contrast, we cannot find any records of *L. albirostris* from New England. On the other hand, the distribution of the two species around the coast of Great Britain is fairly similar, *L. albirostris* being common in the North Sea and occurring also off the Atlantic coasts of Scotland and Ireland, *L. acutus* occurring in the northern part of the North Sea,

round the Orkneys, Shetlands and Outer Hebrides (Matthews 1952, Maxwell 1952).

In Newfoundland the names "jumper" and "squidhound" are used loosely by most fishermen for these two common species of dolphins. Careful observers appear, however, to distinguish the smaller and more active *L. acutus* as "jumpers" and the larger *L. albirostris* as "squidhounds".

In Figures 5 and 6 we have shown corresponding views of the skulls of the two species.

*Grampus orca* (L.). Killer whale. LOCAL NAME: Swordfish

The 17 records of killers in our area are presented in Table III. There is one winter record from Nova Scotia, nine from Newfoundland between April and July, five from Labrador in July and August, and two from offshore waters in October.

Fisher and Sergeant, in a combined total of seven voyages to the seal fishery in March and April, have seen killers only once. C. A. Rose, who has made six voyages, has produced a second record. Both records are cited in Table III. Killers might be expected to occur more numerously amongst the loose ice in April, when live harp seals *Phoca groenlandica* Fabricius, and carcasses left by the sealing ships, would provide much food. Earlier observations indeed suggest that killers were well known at the seal fishery; Carroll (1873) described having seen "swordfish" attack seals at the icefields. Allen (1880) interprets these observations as referring to the true swordfish *Xiphius gladias* L., but they clearly refer to killer whales; the spiked dorsal fin gives the killer this vernacular name in Newfoundland.

M. S. Gordon's records of killer whales in the Strait of Belle Isle in June, 1951, cited in Table III, are supplemented by numerous sight records made by personnel of H.M.C.S. *Labrador* in the same region in June, 1955. These show that many killer whales pass through the Strait, following the large rorquals, somewhat later than the present seal fishery. However, sealing prior to about 1950 often continued into May and June, which suggests why Carroll was familiar with killer whales during the sealing season.

Three single killers taken by Trinity Bay whalers have all been captured in June. A 24-foot male taken on June 28, 1954, contained flesh of a minke whale *Balaenoptera acutorostrata* Lacépède in its stomach, and a 22-foot male taken on June 9, 1956, had been eating seals, probably harp seals. Sergeant, in three summers' observations in Trinity Bay beginning in July each year, has at no time seen killer whales around the abundant pilot whale herds.

Killers were well known to whaling men at the two land-stations of Williamsport, White Bay, in northern Newfoundland and at Hawke's Harbour in southern Labrador, both of which operated up to and including the 1951 season. The late record of a killer near Hawke's Harbour on August 14, 1951, is doubtless to be associated with the whaling activity there. A pack of killers is seen in the whaling sequence of the colour film "The Newfoundland Scene" taken off Williamsport in

1950; these animals were attracted by the blood of a harpooned fin whale *Balaenoptera physalus* L.

The sequence of these records in time and space suggests that killer whales move north through our area in spring and early summer, passing the east coast of Newfoundland in June and Belle Isle Strait in June and July. Probably the majority move north along the Labrador coast to true arctic waters, where they

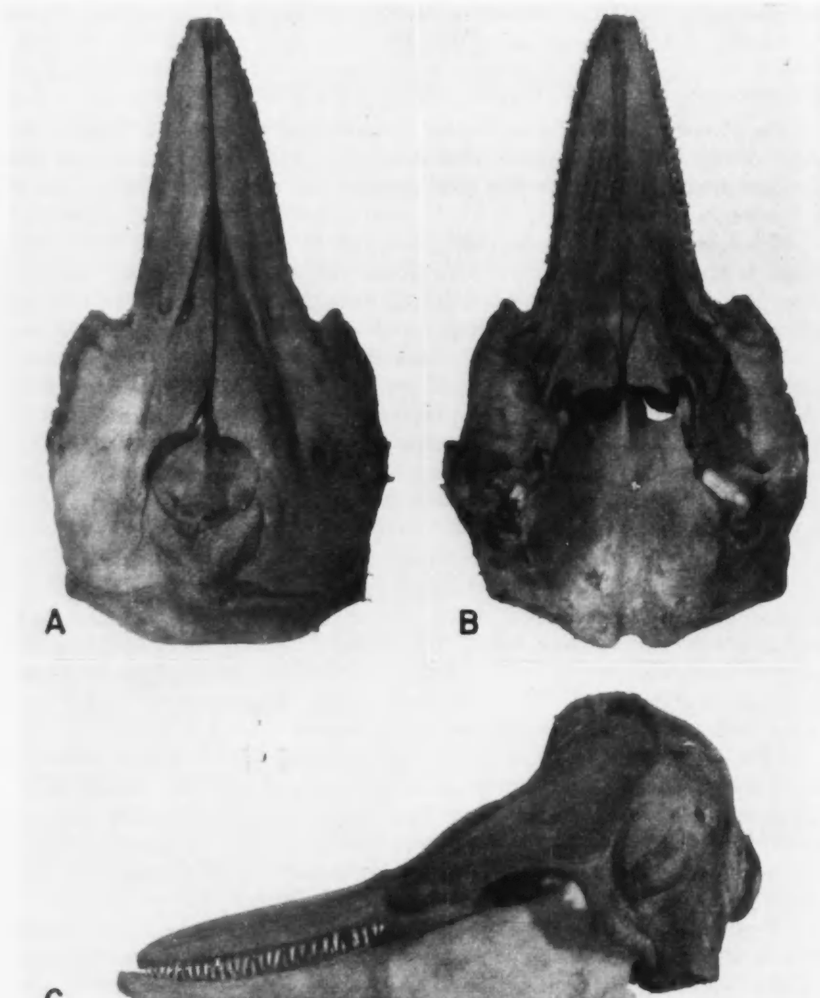


FIGURE 5.—*Lagenorhynchus albirostris*. A, dorsal; B, ventral; and C, lateral views of skull of male, length 216 cm.

are well known, while some may remain farther to the south. The time of movement coincides with that of the rorquals, and it seems likely that these form a prominent part of the killer's food. Vladykov (1944) records that killers prey on herds of white whales in the St. Lawrence estuary in spring and autumn. There is evidently then a return migration of killers into our waters in autumn.

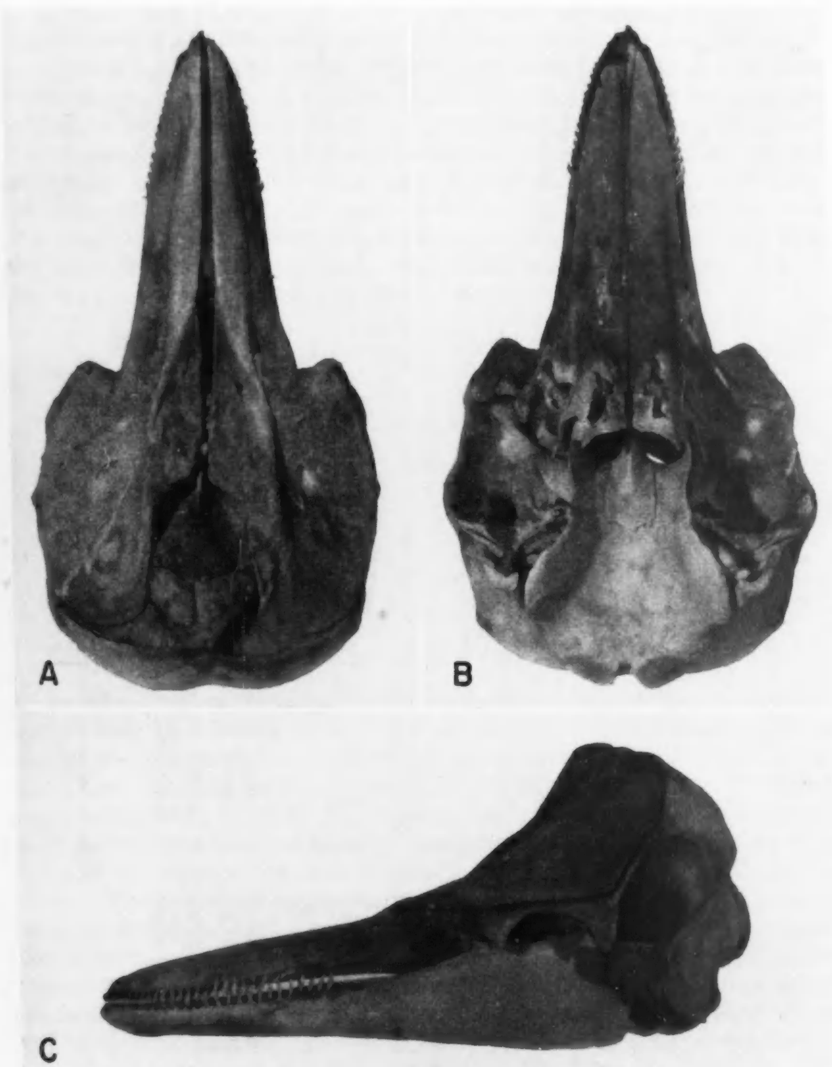


FIGURE 6.—*Lagenorhynchus acutus*. A, dorsal; B, ventral; and C, lateral views of skull of male, length 180 cm.

TABLE III.—Records of killer whales from eastern Canadian waters by months, 1947 to 1954.

| Date | Position: Latitude N. | Position: Longitude W. | Locality | Number in group | Notes | Observer or source |
|---|---|---|---|---|---|---|
| Jan. 4, 1950 | ca. 45°20′ | 63°30′ | Economy, Minas Basin, Nova Scotia | 1 | Stranded | D. Morrison |
| Apr., 1952 | ca. 48°00′ | 53°45′ | Off Southern Baccalieu Island, east coast Newfoundland | 2 | Among loose ice with harp seals | C. A. Rose |
| May 2, 1953 | ca. 51°30′ | 57°00′ | Strait of Belle Isle | 6 | Swimming north along edge of an icefield | H. D. Fisher |
| June 26, 1951 | 50°40′ | 57°20′ | Off Ingornachoix Bay, northwest coast of Newfoundland | 1 | ... | M. S. Gordon |
| June 29, 1951 | 51°35′ | 55°25′ | Between White Islands and shore, Cape Bauld, northern Newfoundland | 1 | ... | " " |
| June 1947 | ca. 47°45′ | 53°40′ | Southern Trinity Bay, east coast of Newfoundland | 1 | Taken by whaling catcher | International whaling statistics |
| June 28, 1954 | " | " | " " | 1 | " | " |
| June 9, 1955 | 47°35′ | 53°40′ | Chapel Arm, southern Trinity Bay, Newfoundland | 1 | Stranded | " |
| July 3, 1951 | 52°13′–53°00′ | 55°50′–55°55′ | Between St. Charles Harbour, St. Lewis Sound and Hawkes Harbour, Labrador | 3 | ... | M. S. Gordon |
| July 5, 1951 | 54°10′ | 58°00′ | In western Hamilton Inlet, Labrador | 1 | ... | " " |
| July 16, 1953 | 53°53′ | 55°53′ | Off Hamilton Inlet, Labrador | 1 | Scavenging round longlining vessel | H. R. Mullett |
| July 17, 1953 | 51°09′ | 57°11′ | Off Ferolle Pt., Strait of Belle Isle | 1 | Scavenging round longlining vessel, eating dogfish | F. K. Spencer |
| July 18, 1954 | 58°00′ | 62°50′ | Just outside Hebron Harbour, northern Labrador | 1 | ... | M. S. Gordon |
| Aug. 14, 1951 | 53°15′ | 56°00′ | About 14 miles north of Hawkes Harbour, Labrador | 1 | ... | " " |
| Oct. 10, 1953 | 56°32′ | 51°00′ | Weather Station "B", Labrador Sea | 4 to 6 | Scavenging round weather ship | ... |
| Oct. 18, 1953 | 56°25′ | 50°50′ | " " | 2 herds 10 to 15 and 7 to 12 | " | ... |

***Globicephala melaena*** (Traill). Pilot whale, blackfish. LOCAL NAMES: Pothead, roundhead

This species visits Newfoundland waters in summer, and must then be the most numerous cetacean. A fishery for "pothead" whales has developed in Trinity Bay since 1947, and several thousand are now taken there each summer. Catches are given in Table IV. A few have been harpooned, but the majority are now taken by driving complete herds on to suitable beaches (Sergeant, 1953).

The sole food of pilot whales in Trinity Bay is the short-finned squid *Illex* (*Ommastrephes*) *illecebrosus* (LeSueur). The squid *Loligo pealii* LeSueur does not occur so far north as Newfoundland. The times of arrival and disappearance of the squid appear to be determined mainly by water temperatures, the preferred range being from about 5 to 15°C. (Frost and Thompson, 1933). The distribution of the pilot whales, closely bound up with that of the squid, is thus fairly simply related to hydrographical conditions. We shall consider, first, their distribution around Newfoundland, where data are most extensive, then in other inshore waters, and lastly in offshore waters.

TABLE IV.—Catches of small whales in Newfoundland, 1947 to 1955.

| Year | Minke (*B. acutorostrata*) | Pilot whale (*G. melaena*) | Killer (*G. orca*) | Bottlenose (*H. ampullatus*) | Dolphin *Lagenorhynchus* |
|---|---|---|---|---|---|
| 1947 | 16 | ... | 1 | ... | ... |
| 1948 | 41 | 15 | ... | ... | 2[a] |
| 1949 | 38 | ... | ... | ... | ... |
| 1950 | 3 | 172 | ... | ... | ... |
| 1951 | 55 | 3,100 | ... | ... | ... |
| 1952 | 17 | 3,155 | ... | ... | ... |
| 1953 | 25 | 3,584 | 1 | 1 | ... |
| 1954 | 32 | 2,298 | 1 | ... | 2[b] |
| 1955 | 13 | 6,412 | 1 | ... | ... |

[a]Probably *Lagenorhynchus albirostris.*
[b]Certainly *Lagenorhynchus acutus.*

In most summers squid appear on the southwest edge of the Grand Bank in early May to mid-May. This is the area around Newfoundland with the warmest water in spring. Our earliest date for the arrival of pilot whales on the Grand Bank is not, however, until June 27, both in 1953 at 42°50′N., 50°00′W. and in 1954 at 43°00′N., 50°55′W. The latter record comes from E. M. LeGrow, on board the Fisheries Research Board's *Investigator II,* who noted that squid were on top of the water at the time. A possible reason for the later arrival of the whales is that the squid are apparently in deeper water in May and June, as shown by records of water temperatures and accompanying catches of squid taken in fine meshed trawls by the *Investigator II.* Pilot whales are seen on the southern Grand Bank throughout the summer months and remain there up to late autumn; an exceptionally late winter record is from 42°30′N., 52°00′W. in the first week of January, 1953, when many pilot whales were seen and two squid taken in large-meshed nets by the trawler *Blue Foam.* This was a year of marked Gulf Stream influence.

Our earliest date for the arrival of pilot whales in Newfoundland coastal waters is June 26, 1954, when three herds were seen in Hermitage Bay on the south coast by E. J. Sandeman. The first herds arrive in Trinity Bay a little later, a few days after the first squid strike in at the squid-jigging grounds at the heads of the bay. Again the last roaming bands are seen shortly before the last squid disappear from these places. Dates for these phenomena in recent years are shown in Table V.

TABLE V.—Dates of arrival and departure of squid and pilot whales in Trinity Bay.

| Year | Squid seen | | Pilot whales seen or taken | |
|---|---|---|---|---|
| | First | Last | First | Last |
| 1951 | ... | ... | July 21[a] | November 6 |
| 1952 | ... | ... | July 12[a] | November 8 |
| 1953 | June 22 | November 10 | July 8 | November 4 |
| 1954 | June 30 | November 16 | July 6 | November 10 |
| 1955 | July 12 | October 30 | July 15 | October 22 |

[a]Dates prior to 1953 probably do not indicate the first appearance, since catching effort was then restricted early in the season.

Pilot whales are found most regularly in the deeper bays of Newfoundland, e.g. Hermitage, Fortune, Conception, Trinity, Bonavista, Notre Dame and White Bays, with later arrivals in the more northerly of those mentioned. They seem to be irregular, or to remain for a shorter time, on the southwest and southern part of the west coast of the island, as in the Bay of Islands and St. Georges Bay. This may perhaps be correlated with a general scarcity of squid on the west coast. We have records, however, from Ingornachoix Bay on the northwest coast in 1953, when a very large herd of pilot whales mixed with tuna *Thunnus thynnus* L. was seen by F. Spencer on August 12, and in mid-October, 1955, when one herd of 250 was seen west of the Port-au-Port Peninsula by E. M. LeGrow.

It is difficult to delimit the summer range, since it doubtless varies from year to year with the variable distribution of squid. As shown by Frost and Thompson (1933, 1934), squid are sometimes at a maximum on the east and southeast coast, sometimes on the south coast. The long history of pilot-whale driving in Trinity Bay, and to a lesser extent also in Bonavista and Hermitage Bays, suggests, however, that the most regular occurrence of squid and whales is on the southern part of the east coast and eastern part of the south coast. For the same reason the effect of the recent warm period on distribution is hard to assess; the only clear effect of this period, which dates from about 1940 in Newfoundland, has been to bring about an earlier arrival of squid in summer on the east coast. In the 1920's they arrived in Bonavista Bay in August, now in early July (information from Dr. W. Templeman).

The extent of these variations on distribution may be exemplified by data for the two years 1954 and 1955. In the summer of 1954 calm summer weather produced an abnormally thin and stable layer of warm surface water around Newfoundland and apparently along much of the Labrador coast also (Annual Report of the Fisheries Research Board of Canada for 1954, p. 59). The squid

extended far to the north, at least to Hamilton Inlet Bank and Hebron Fjord (see below). Pilot whales were present in Trinity Bay from early July to early August, thereafter became scarce and were totally absent between September 4 and October 29. Three drives were again made in Trinity Bay between October 29 and November 6, and one of over 200 whales in Bonavista Bay on October 18. Meanwhile pilot whales were abundant on Hamilton Inlet Bank at 54°40′N., 53°30′W. from September 6 to 19, as recorded by E. M. LeGrow on the *Investigator II*, and the party on board the research vessel *Calanus* that summer recorded two "almost certain" pilot whales off Port Burwell in Ungava Bay on August 20 (field notes of Dr. M. J. Dunbar). This party found squid abundant in Hebron Fjord in early September. In late September newspaper reports indicated that many squid had stranded on the shore in White Bay, and that pilot whales at the same time were common in Notre Dame and White Bays. Statistics of squid landings in Conception Bay in July, August and September, 1954, showed that the squid retained their normal abundance in this area throughout the summer. Thus it appears that the pilot whales, which carried out an unusually marked migration northward in summer, followed the stocks of squid which moved farther to the north. In 1955, on the other hand, the distribution of both squid and whales was restricted; squid were recorded no farther north than Quirpon in northernmost Newfoundland, and pilot whales were present in great numbers all the summer in Trinity and Bonavista Bays, giving a record commercial catch (Table IV).

In some years squid and whales have failed entirely to enter Newfoundland inshore waters. Data presented by Templeman and Fleming (1953) show almost or complete absence of squid in 10 different years between 1901 and 1950, or about one year in four, but without any detectable regularity. There may be failures in two or three consecutive years, the last such being in 1948 and 1949 when few or no squid were taken on the east coast. As a result, in 1948 only 15 pilot whales were taken in Trinity Bay, and in 1949, none. In this second year, however, gunners from the Williamsport whaling station reported seeing pilot whales a few miles offshore in White Bay. This suggests that absences may be local only, and not failures of one or more broods of squid. There is, however, no correlation of the 1948–49 scarcity with summer water temperatures, and no other hydrographical correlates have yet been detected.

The fluctuations are of importance to the new mink-ranching industry of southern Trinity Bay which is dependent largely on pilot whales as a source of meat, and must be ready to turn to other species of whales should a failure recur. At present, the arrival of pilot whales in any summer can only be forecast two months ahead when the arrival of squid on the Grand Bank in May seems always to be followed by inshore appearance of squid and whales in July.

On the Atlantic coast of the Maritime Provinces, pilot whales are not commonly seen in inshore waters. A herd stranded at St. Mary Bay, near Digby, N.S., on August 2, 1949, was recorded by J. C. Medcof, and a single stranded pilot whale near Yarmouth in early August, 1954, was recorded by W. Klawe. During a cruise of the oceanographic research ship *Sackville* off the southern coast of

Nova Scotia in 1954, H. J. McClellan recorded a school of about 40 pilot whales near Georges Bank at 41°58′N., 65°49′W. on October 9, and a similar number near Banquereau at 44°08′N., 58°10′W. on October 21. The surface temperatures during these sightings were respectively 12 and 14°C.

In the southern Gulf of St. Lawrence, pilot whales were reported by S. N. Tibbo in all the shallow water areas in the four years 1950 to 1953. In September, 1953, they were common from the neighbourhood of the Magdalen Islands to Gaspé, and especially on American Bank. J. W. Saunders recorded a stranded animal at Grande Rivière, Gaspé, in 1953 when squid were present. The same observer reported that while pilot whales were formerly common around Sydney, Cape Breton Island, none had been seen between about 1947 and 1953. The only earlier published records from the Gulf are from the years 1930, 1934 and 1936. Needler (1931) reported a herd of 200 pilot whales stranded at the mouths of Percival and Enore Rivers, on the south coast of Prince Edward Island, on August 29, 1930, and about 50 on the shore near Borden, P.E.I., on August 15 or 16 of the same year, while some one to two dozen were seen swimming in the harbour at Summerside, P.E.I., on October 4. Other reports of pilot whales were obtained, and Needler wrote: "There is no doubt that in the summer of 1930 they were unusually abundant in Northumberland Strait where they had not been seen for many years".

In the same summer pilot whales entered the estuary of the St. Lawrence. A herd of 21 was stranded at Trois Pistoles, on the south shore opposite the mouth of the Saguenay River, on August 31, 1930. Préfontaine (1930), who reported this visitation, wrote that the species was previously unknown locally. The stomach contents of a specimen examined by him were the amphipod *Gammarus locusta* L. and the squid *Loligo pealii;* the squid had been abundant along the banks of the estuary some days before the stranding occurred, this too being a rare occurrence. Préfontaine also recorded that two individual pilot whales were found later at Boischatel, Ile d'Orléans, in the first week of October and at St. Anne de la Pocatière on October 16, the first locality being the upstream limit of penetration of saline water at highest spring tides.

Mathewson (1935) also recorded strandings in the estuary in 1934: a herd of 23 at Métis, eight around Tartague and Rivière Blanche, and 40 at Boule Rock sandbank, all in early September. These localities are on the Gaspé shore somewhat below the area of strandings in 1930. Vladykov (1944) recorded a further incursion in 1936, larger than that of 1934 but smaller than that of 1930.

The data suggest that while incursions occurred sporadically in the Gulf and estuary of the St. Lawrence in the past, there may have been a more extensive penetration of the Gulf by pilot whales in the last decade. Not knowing, however, whether their food in this region is *Illex* or *Loligo*, we cannot correlate this with possible hydrographical changes. It may be, as Vladykov suggested, that they occur in years of marine transgressions, and if so one would look for comparative data on salinities to correlate with penetration of the oceanic *Illex* into less saline waters.

The normal range of *Loligo pealii* is from South Carolina to Nova Scotia (Verrill, 1881), and it is a species which breeds in shallow rather than deep

water. *Illex illecebrosus coindeti*, the form of this species which inhabits the western North Atlantic, ranges from the Gulf of Mexico to our area as delimited above (Voss, 1955), while there are single records for Cumberland Sound, Baffin Island (Verrill, loc. cit.) and from Frederikshaab, West Greenland (Posselt, 1898). It is primarily an offshore species and is believed to breed in or over deep water. Off Cuba in spring it is found at depths of 180 to 260 fathoms (Voss, loc. cit.). In our area, an inshore movement of *Illex* in the surface waters takes place regularly only around Newfoundland, although a similar movement may occur rarely in Passamaquoddy Bay, as in September–October, 1955. It is only around Newfoundland, too, that the northern pilot whale occurs inshore with regularity. It seems probable, then, that *Illex* is the main food of this whale throughout its western north Atlantic range. However, we have no knowledge of its feeding habits in offshore waters.

Considering the oceanic range of pilot whales in offshore waters east of Canada, observations from Weather Station "B" show that pilot whales are common in that region between early July and the end of October (Table VI). Observations regarded as reliable were obtained from July 9, 1953, through all summer months up to October 28, and again on July 5, 1954, just before observations ceased. None were observed from October 30 to November 11, 1953, and there were no observations sent in through December, January and February. Two records in March, 1954, are unsupported by details and must be considered doubtful. This season of occurrence in offshore waters of the boreal North Atlantic is thus the same as the season in inshore waters of Newfoundland. Herds seen at Station "B" during the summer contained between 10 and 100 animals. Large herds on October 10 (two of 60 and 140), and October 28 (one of 100), suggest a gathering together before migration.

Observations from Station "D" (Table VII) showed pilot whales to be present in 1954 from September 25 to October 6 and December 2 to 13; in 1955 from January 10 to 12, February 7 and 8 and June 30 to July 2, and there is again a record of a herd on September 15. None were observed in cruises during April and the greater part of June, and records are lacking in other months. In spite of less intensive observation at "D" than at "B", and the greater possibility of confusion with other species such as *Grampidelphis griseus* (Gervais) in a warmer water region, it seems likely that pilot whales are present at "D" through the winter months from about mid-September to early July.

To summarize our knowledge of pilot whale distribution in inshore and offshore waters: pilot whales summer commonly in coastal waters from Cape Breton Island north to southern Labrador and in the Gulf of St. Lawrence, rarely reaching the estuary of that river; they do not penetrate commonly into coastal waters farther south in the Maritime Provinces; they also summer over deep water in the central Labrador Sea; they move outside the Continental Shelf in winter, and are then known to occur east of the Grand Bank in North Atlantic Current waters.

Jensen (1939) recorded details of the occurrence of pilot whales in Greenland waters during recent decades. These have been supplemented for the post-war years by Dr. Poul Hansen, in a letter to Sergeant of September 1, 1954.

TABLE VI.—Records of pilot whales from weather station "B" and other parts of the Labrador Sea, 1953 to 1954.

| Date | Position | | Locality | Number in herd | Notes | Observer | U.S.C.G. vessel |
|---|---|---|---|---|---|---|---|
| | Latitude N. | Longitude W. | | | | | |
| 1953 | | | | | | | |
| July 9 | 52°32′ | 51°38′ | S. of "B" | ca. 10 | ... | R. A. Whipple | *Half Moon* |
| July 11 | 54°58′ | 52°31′ | SW. of "B" | ca. 15 | Stationary and feeding | " " | " " |
| July 15 | 56°32′ | 51°00′ | At "B" | 80 to 120 | In company with dolphins | " " | " " |
| Julu 18 | 55°02′ | 51°20′ | " | 12 | Travelling | J. T. Allison | *Unimak* |
| July 22 | 56°30′ | 51°00′ | " | 60 to 70 in 5 herds | Stationary, many calves seen | " " | " |
| Aug. 3 | 56°33′ | 51°05′ | " | 30 to 40 in 2 herds | Travelling. Photographed | " " | " |
| Aug. 4 | 56°28′ | 50°46′ | " | 100 in herds of 20–30 | In company with dolphins | " " | " |
| Aug. 10 | 56°26′ | 51°03′ | " | 50 | Travelling | Many observers | *Sebago* |
| Aug. 26 | 56°27′ | 50°49′ | " | 100 | Travelling | " " | " |
| Aug. 27 | 56°30′ | 51°00′ | " | 25 | Feeding | " " | " |
| Sept. 4 | 56°12′ | 50°20′ | " | 20 | Travelling | E. F. Trainor | *McCulloch* |
| Sept. 14 | 57°27′ | 51°52′ | " | 9 | Feeding | " " | " |
| Sept. 15 | 57°49′ | 50°54′ | " | 30 | Feeding | " " | " |
| Sept. 21 | 56°30′ | 51°00′ | " | 30 | Feeding | Officers of the deck | *Chincoteague* |
| Sept. 28 | 57°30′ | 52°40′ | " | 25 | Travelling | " " " | " |
| Oct. 10 | 56°30′ | 51°07′ | " | 200 in herds of 60 and 140 | Travelling WNW. at 5 knots | L. B. Smith | *Humboldt* |
| Oct. 28 | 56°16 | 51°07′ | " | 100 | Travelling SE. at ca. 5 knots | " " | " |
| Oct. 30–Nov. 20 | ... | ... | " | ... | (Snow showers) | ... | *Spencer* |
| 1954 | | | | | | | |
| Mar. 5–14 | ... | ... | " | ... | ... | Many observers | *Spencer* |
| Apr. 17–May 8 | ... | ... | " | ... | Much fog, sleet and snow | W. T. Barber | *Cook Inlet* |
| May 8–28 | ... | ... | " | ... | ... | Officers of the deck | *McCulloch* |
| July 5 | 56°30′ | 51°00′ | " | 30 to 40 | Travelling | " " " | *Absecon* |

TABLE VII.—Records of pilot whales *Globicephela* from weather station "D", east of the Grand Bank, 1954 to 1955.

| Date | Position: Latitude N. | Position: Longitude W. | Number in herd | Notes | Observer | U.S.C.G. vessel |
|---|---|---|---|---|---|---|
| 1954 | | | | | | |
| July 3 | 45°30′ | 44°00′ | ... | ... | J. Copin | *Half Moon* |
| July 17 | 43°50′ | 41°00′ | ... | Dolphins seen | " " | " " |
| July 25 | 45°30′ | 46°30′ | ... | ... | " " | " " |
| Sept. 25 | 44°03′ | 40°57′ | 40 | Travelling | McK. Greenley | *Spencer* |
| Oct. 3 | 43°43′ | 41°21′ | 70 | Stationary | " " | " |
| Oct. 5 | ... | ... | 50 | Travelling | " " | " |
| Oct. 6 | 44°10′ | 41°00′ | 32 | " | " " | " |
| Oct. 22 | 44°13′ | 41°00′ | ... | Dolphins seen | G. A. Holmes | *Unimak* |
| Dec. 2 | 44°00′ | 41°00′ | 20 | Travelling | Many observers | *Mendota* |
| Dec. 11 | " | " | 20 to 25 | Feeding | " " | " |
| Dec. 13 | " | " | 50 | Travelling | " " | " |
| 1955 | | | | | | |
| Jan. 10 | 44°00′ | 41°00′ | 25 to 30 | Travelling slowly | Officers of the deck | *McCulloch* |
| Jan. 12 | 43°50′ | 41°05′ | 25 to 30 | ... | " " " | " |
| Feb. 7 | 43°54′ | 40°44′ | 4 | Travelling | J. W. McCook | *Chincoteague* |
| Feb. 8 | 43°50′ | 41°12′ | 20 | " | " " | " |
| April | On station | On station | ... | ... | J. M. O'Connell | *Barataria* |
| June 6–21 | On station | On station | ... | Dolphins seen | Many observers | *Bibb* |
| June 30 | 44°08′ | 40°52′ | 30 | Travelling. Sea temp. 20°C. (68°F.) | ... | ... |
| July 2 | 44°12′ | 41°15′ | 6 | Travelling. Sea temp 21.6°C. (71°F.) | ... | ... |
| Sept. 8 | 44°05′ | 41°05′ | 50 | Feeding, a few porpoises associated | G. A. Holmes | *Unimak* |

From 1926 to 1953 there were some 20 sight-records, strandings or drives of pilot whales in West Greenland, extending from off Kap Farvel in the south to Disko Bugt in the north. All records but one were from June to late October, with the majority in September. The exception was a herd which overwintered near Godthaab in 1931–32. Records are from the years 1926, 1928, 1931–32 (especially), 1935, 1946 and 1953. The species was unknown before the present warm period, and the records show a general correlation with increased summer temperatures. Smed (1953, 1954) shows that the surface temperatures in West Greenland waters from 1926 to 1937 and from 1945 to 1953 were warmer than the 1876–1925 average with 1938 a cold year and data missing during the war years. According to Hansen, a fishery for pilot whales has developed in West Greenland, but since it is rather new it is less highly organized and less successful than the fisheries in the Faeroe Islands or in Newfoundland. The food of pilot whales in West Greenland is not known. The common species of squid is *Gonatus fabricii*. According to Dr. Hansen, small specimens of this species are abundant in the summer plankton and extend north to about 68 or 69°N. Lat. The adults have not been taken in shoals. Hansen had not met with *Illex* in the recent warm period, but there is a single record of the species from West Greenland in the nineteenth century, as mentioned above. Thus it seems possible that visitations of pilot whales to West Greenland may follow occasional invasions of *Illex* in warm summers. Dr. Erik Smidt, director of the Fiskeri-biologisk Laboratoriet at Godthaab adds that pilot whales generally stay offshore in West Greenland waters (information sent to Sergeant per Mr. D. V. Ellis, in a letter of May 31, 1956). Since surface temperatures of the West Greenland fjords are somewhat lower than those over the coastal banks, this information is in general agreement with our conclusions as to the temperature preference of pilot whales around Newfoundland.

In European seas, *Globicephala melaena* occurs numerously between Iceland, the Norwegian coast and Great Britain in summer, with its maximum concentration around the Faeroe Islands (see, for instance, Norman and Fraser, 1949). As to the food of pilot whales in these waters, Saemundsson (1939) writes that they pursue the squid *Ommatostrephes sagittatus* (Lamarck) into the Icelandic fjords. This squid has a range in the northeast Atlantic very similar to that of *Illex illecebrosus* in the northwest (Grimpe, 1933), and appears to have very similar habits, forming large shoals in the surface waters and often coming to shore.

The Trinity Bay pilot whales, some 3,700 of which were examined by Sergeant in three summers show almost no variation in colour pattern. The ventral markings consist of a shield-shaped patch of elephant grey on the throat leading into a narrow grey stripe along the mid-ventral line of thorax and abdomen. Within this area the grey expands around the navel, while the inguinal region of the male and the teats of the female are both surrounded by a zone of white (Fig. 7A). The rest of the body is slate-grey when wet and dark chocolate when dry. Newborn animals 6 to 7 ft. (180 to 210 cm.) in length have not fully developed their pigmentation, and have a medium-grey body colour. Occasionally individuals of up to 10 ft. (300 cm.) are markedly paler than the average. The pale

area behind the dorsal fin, found in some large males and females, is mentioned below.

In this coloration Newfoundland pilot whales resemble closely typical *G. melaena* from northern European seas. (Compare Fig. 7A with fig. 2, p. 28 in Fraser (1953) and with fig. 1–3 and plate 5 of Williamson (1949).) We do not have enough data from Europe to compare mean lengths, but our extreme lengths of 20 ft. 3 in. (617 cm.) for males and 16 ft. 9 in. (511 cm.) for females correspond with extreme lengths for smaller numbers of stranded whales in Britain given by Fraser (1953). In a stranding at Westray, Orkney Islands, in March, 1955, the largest of 15 measured males was 20 ft. 6 in. (625 cm.) in length and the largest of 22 females 17 ft. 7 in. (536 cm.), suggesting a somewhat larger mean size. (Data kindly sent by Mrs. L. de Kock of Marischal College, Aberdeen, Scotland.)

Our samples may also be compared with two smaller samples from the Gulf and estuary of the St. Lawrence measured by Needler and Préfontaine (loc. cit.) in the summer of 1930. Needler recorded males up to 22 ft. (671 cm.) and females up to 18 ft. (549 cm.) in standard length, in a sample of 94; Préfontaine, males up to 21 ft. (640 cm.) in a sample of 19. Needler's mean lengths were 17 ft. 6 in. (533 cm.) for males, 14 ft. 6 in. (442 cm.) for females. The Newfoundland whales show mean lengths of 13 ft. (396 cm.) for both sexes in unselected samples totalling over 3,000 animals. The Gulf herds were thus certainly composed of larger animals.

Pilot whales have been stranded fairly often around Cape Cod (True, 1889; Starrett and Starrett, 1955), and it would be of great value if a study of measurements, feeding and breeding biology could be made on herds stranded there in the future. It would also be of value to delimit the zone of interchange between *G. melaena* and the subtropical *G. macrorhyncha* (Gray) (=*G. brachytera* Cope) on the eastern United States seaboard. The latter species differs from *G. melaena* in its darker coloration and in the form of its skull, which has the maxillae expanded dorsally over the premaxillae (Fraser, 1950). It is well known off Florida (Kritzler, 1952; Moore, 1953), and the Leeward Islands, where there is a small fishery (R. S. Rack, letter to Sergeant of October 21, 1954). True (1889) recorded one specimen (Cope's type of *G. brachyptera*) from Delaware Bay, and one from Virginia, in the collection of the United States National Museum, as well as three from Florida. These data suggest that the zone of interchange may lie about off New York.

*G. melaena* resembles the species *G. leucosagmaphora* Rayner of the Southern Oceans much more closely than *G. macrorhyncha;* indeed, the southern species was formerly not distinguished from the northern. The two are closely similar in skull form and coloration. An interesting similarity in colour pattern, not apparently noted in the literature, was pointed out by Mr. W. B. Schevill on examination of Newfoundland specimens of *G. melaena*. In a percentage of the large males and females there is a triangular area of grey, lighter than the general dark colour, behind the dorsal fin (Fig. 7B). This saddle is found in most specimens of *G. leucosagmaphora* (Scott, 1942), and gives the species its

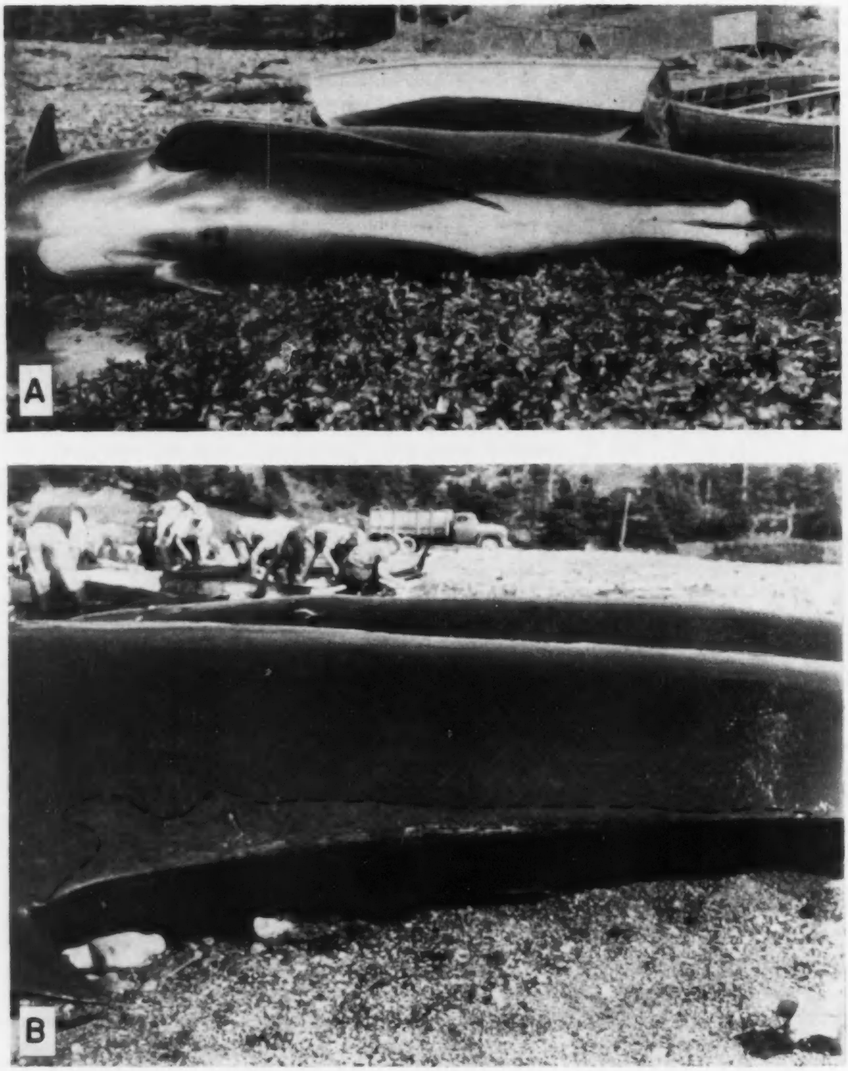


FIGURE 7.–*Globicephala melaena*. A. Ventral view of adult female to show colour pattern. B. Dorsal view of adult female showing grey "saddle".

name (Rayner, 1939). *G. macorhyncha* is uniformly dark dorsally and the ventral pattern though visible is darker and less clearly distinguished than in the two species of colder waters.

The skull of a large male pilot whale from Newfoundland is shown in Figure 8.

A detailed life-history study of pilot whales, studied by Sergeant in Trinity Bay, is in preparation.

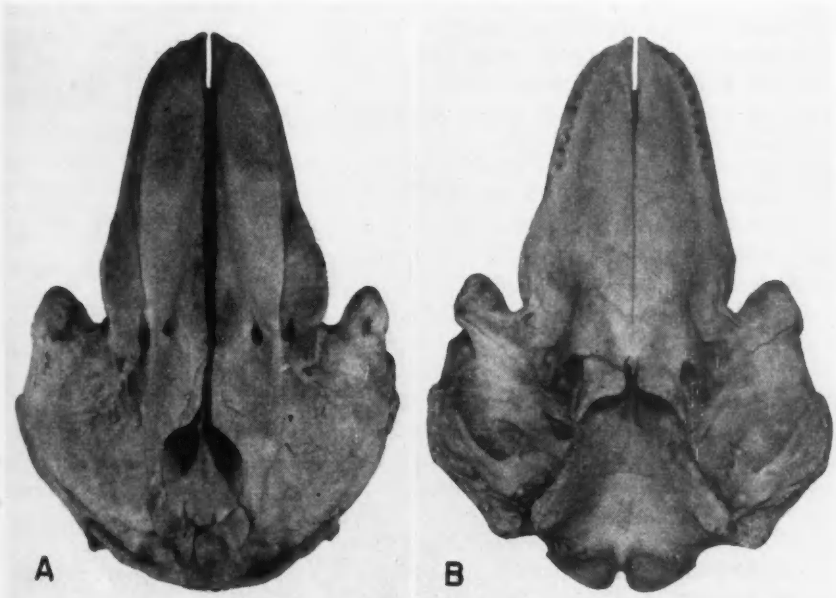


FIGURE 8.—*Globicephala melaena*. Left, dorsal and right, ventral views of skull of male, length 580 cm.

***Phocoena phocoena*** (L.). Common porpoise. LOCAL NAME: Puffing pig

Each year in June large numbers of the common porpoise appear in the waters just outside the entrance to Passamaquoddy Bay and along the west side of the Bay of Fundy at least to Musquash. Fair numbers enter Passamaquoddy Bay itself and range into the lower reaches of the St. Croix River estuary. They remain numerous throughout the summer, become scarce after September and by November have largely left the area. Herring *Clupea harengus* L. has been found to be the principal item of diet during this time, but squid *Loligo pealii*, hake *Urophycis tenuis* (Mitchill), and pollock *Pollachius virens* (L.) are commonly taken (unpublished studies by H. D. Fisher). The porpoise is well-known

elsewhere in the Maritimes but little is known of its seasonal movements or habits, except that it is not found during winter months.

In Newfoundland, porpoises are well-known to the inshore fishermen, being frequently taken in cod traps in June and July. We have seen small groups, usually two to three in number, in southern Trinity Bay from late May to late July, and have seen one dead specimen there: a young male, length 4 ft. 2 in. (127 cm.) taken in a cod trap at Dildo on July 9, 1952. It is certain that porpoises desert Trinity Bay in summer for we have never observed them after late July. Their distribution elsewhere in Newfoundland and Labrador waters is unknown; we have records from Placentia Bay in early July, 1954, in White Bay in September and October, 1953, and general reports from the Labrador coast in summer. Nothing is known of their food in this area, but it seems likely from their season of occurrence in Trinity Bay that capelin are sought after.

## SUMMARY

1. An account is given of the known records, distribution, abundance and migrations of the smaller toothed whales known from eastern Canadian waters, with measurements of specimens of the rarer species.

2. The following species are added to the Canadian fauna: Sowerby's whale *Mesoplodon bidens* (Sowerby), the bottle-nosed dolphin *Tursiops truncatus* (Montague), the white-beaked dolphin *Lagenorhynchus albirostris* (Gray), and the white-sided dolphin *L. acutus* (Gray).

3. The status of the above species and of the following is discussed, following citation of sight-records, strandings and catches: the common dolphin *Delphinus delphis* L. killer whale *Grampus orca* (L.), white whale *Delphinapterus leucas* (Pallas), common porpoise *Phocoena phocoena* L., and, in most detail, pilot whale *Globicephala melaena* (Traill).

4. Records of killer whales are distributed in a way which suggests that this species migrates northwards along the Canadian Atlantic coast in spring and early summer. This migration parallels the migration of the rorquals, on which the killer whale is known to prey in these waters.

5. The white-sided dolphin is frequently associated with the pilot whale in these waters. This fact, together with the season of its occurrence in Newfoundland waters, suggests that it is a species of boreal waters. In contrast, evidence is presented which suggests that the white-beaked dolphin may prefer colder waters.

6. Northern pilot whales are abundant in summer in inshore waters from Cape Breton Island north to the Strait of Belle Isle and west into the Gulf of St. Lawrence, with maximum abundance on the southeast coast of Newfoundland. In warm summers the migration may reach mid-Labrador. This distribution is directly dependent on the distribution of the short-finned squid *Illex illecebrosus* (LeSueur), which forms the sole food of the pilot whales occurring in eastern Newfoundland waters in summer. Pilot whales also occur offshore in the Labrador Sea in summer. There is thus an oceanic as well as a denser inshore population

at this time. In winter the species migrates outside the waters of the Continental Shelf and is known to occur east of the Grand Bank in North Atlantic Current waters. In some summers squid and pilot whales, for reasons not understood, fail completely to come inshore in Newfoundland.

7. Some further similarities of the northern pilot whale to the southern species *G. leucosagmaphora* Rayner are noted.

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